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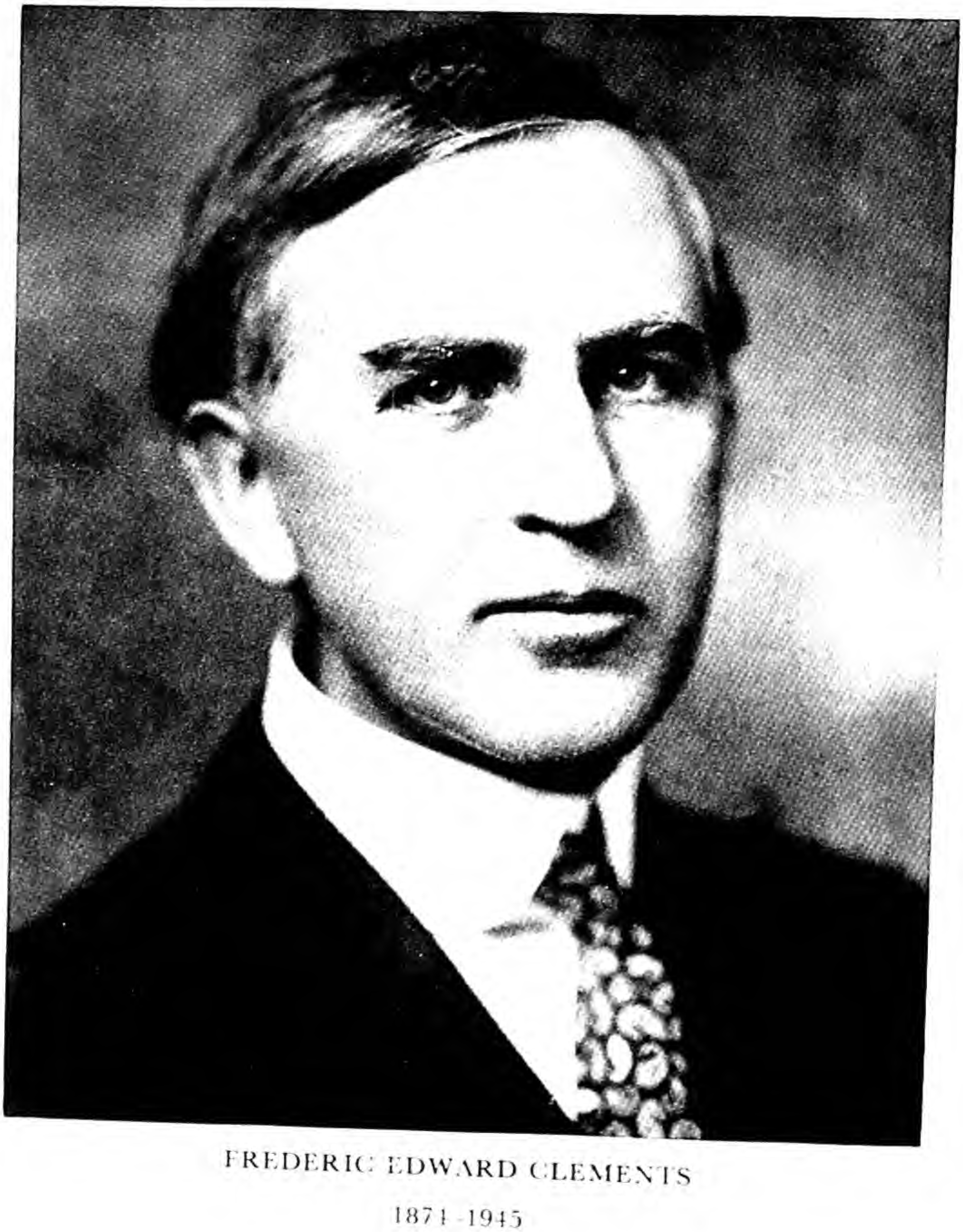

FREDERIC EDWARD CLEMENTS

1874–1945

DYNAMICS OF VEGETATION

Selections from the Writings of

FREDERIC E. CLEMENTS, PH.D.

Compiled and Edited by

B. W. ALLRED

Chief, Regional Range Division, Soil Conservation Service, Fort Worth, Texas

AND

EDITH S. CLEMENTS, PH.D.

Author and Illustrator

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PREFACE

This book, DYNAMICS OF VEGETATION, is a compilation of selected writings on Dynamic Ecology by Dr. Frederic E. Clements, for which there is a widespread and continuing demand. It has been undertaken with the twofold purpose of serving as a memorial to Dr. Clements' creative genius in the field of ecology, and to make available a number of his most important and out-of-print contributions, as serviceable references and guides to agronomists, range men, biologists, foresters, conservationists, teachers and students.

Dr. Clements had the good fortune to be a pioneer in the development of the kind of ecology based on experiment and measurement of the factors in the environments of living organisms. Endowed with a passion for research, a keenly analytical mind and unusual opportunities afforded by connection with the Carnegie Institution of Washington for many years, he was generally acknowledged to be the leading exponent of what has come to be known as "Dynamic Ecology."

His first studies of vegetation were made in 1893, at the age of nineteen, when he made a preliminary survey of the State of Nebraska. This was followed by later explorations in collaboration with Dr. Roscoe Pound, and the results were published in 1898 under the title "The Phytogeography of Nebraska," after having been presented as a thesis for the Doctor's degree.

After serving on the faculty of the University of Nebraska until 1907, he accepted the position of Head of the Department of Botany in the University of Minnesota. His experience with students in both universities led to the conviction that lectures and note-books were hindrances rather than helps in the acquisition of knowledge, with the result that both were dispensed with in his classes and the student put to work directly with living material in laboratory and greenhouse. The outcome proved the soundness of this judgment and established Dr. Clements as outstanding in the field of education.

Mrs. Clements, who had taken a Doctor's degree in Ecology at the University of Nebraska, worked side by side with her husband, contributing in no small degree to his undertakings, as well as gaining recognition in her own right as an illustrator and writer of popular books on

wild-flowers. Both the Doctors Clements spent summer vacations during the period of university teaching, in research in laboratory and gardens at a midalpine station on Pikes Peak, and in extensive travel throughout the West and Middle West, with one summer in Europe when they were members of an International Geographical Excursion.

The results of the study of vegetation at large were ready for publication by 1915, and at the suggestion of Dr. D. T. MacDougal of the Desert Laboratory of the Carnegie Institution of Washington, were presented to the President and Board of Directors of that Institution. The manuscript was approved by them and published in 1916 under the title "Plant Succession." Shortly thereafter Dr. Clements was appointed Associate of the Carnegie Institution, with freedom to devote all his time to research, and with adequate funds for travel and laboratory facilities, as well as assistants.

Two stations for research in ecological problems were established eventually; an alpine laboratory on Pikes Peak for summer work, and a coastal laboratory and gardens at Santa Barbara, California, where mild winters made year round experimentation possible. These intensive studies of the behavior of plants under controlled conditions were supplemented by half a million miles of automobile travel back and forth across the continent, and from Mexico into Canada, and results have appeared during the years in a large number of publications. It is from these that the material for this book has been taken.

The chapters dealing with plant succession, and farm, forest and range plant indicators were drawn from the two classics, "Plant Succession," 1916, and "Plant Indicators," 1920. These books are out of print, but an abridgment of the two is still available under the title "Plant Succession and Indicators," published in 1928.

The chapter on "Climatic Cycles and Human Populations in the Great Plains" is taken from the Scientific Monthly, September, 1938. This is a brilliant essay on the Great Plains which have been regarded as a calamity area for generations. It gives a view of Dr. Clements' clairvoyance in methods of weather analysis that are indispensable in interpreting regional economics and land use. He points out that the "Great Plains" is a region of latent opportunity if properly used.

The chapters on "Nature and Structure of the Climax" and "The Relict Method in Dynamic Ecology" are taken from the Journal of Ecology. They present a rich background of ecological science and per-

tain to the classification of plant communities and to methods for determining what plants are native to an area after disturbance has taken place. They set forth the fundamental principles of ecology as applied to understanding and solving practical problems connected with vegetation. Plant communities are classified as simply as human communities, and the earlier climax can be reconstructed from relicts left by its disappearance.

The remaining chapters deal with conservation and the application of ecological concepts and methods to fields in which plants furnish the working materials, such as landscaping, forestry, soil conservation, range management and similar objectives. Dr. Clements brought to these subjects the knowledge and experience gained through many years active association with men at work in the field. His students had been put in charge of five of the western Forest Experiment Stations and for the past ten years or so of his life, he spent much time with soil conservationists discussing their problems on the ground, and making helpful suggestions. The content of this book, in consequence, represents a broad philosophical outlook, combined with practical experience that should make it a worthwhile contribution to scientific knowledge and its practical application.

Acknowledgments for helpful suggestions and encouragement in undertaking this project are due Dr. D. T. MacDougal, formerly of the Carnegie Institution, Dr. W. S. Cooper of the University of Minnesota, Dr. J. E. Weaver of the University of Nebraska, Dr. C. H. Muller of the Santa Barbara branch of the University of California, and especially Mr. Bernhard Hoffmann of Santa Barbara, California, who suggested the desirability of such a publication in the first place.

Credit for the photographs used as illustrations is due Dr. Edith S. Clements, with the exception of those in Chapter II which were made by Dr. J. E. Weaver, and a few from the Soil Conservation Service and U.S. Geological Survey which have been so indicated on the individual reproductions.

B. W. Allred.

Soil Conservation Service
Fort Worth, Texas
October 23, 1948

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Dynamics of Vegetation

Chapter I

PLANT SUCCESSION AND HUMAN PROBLEMS

1. The Nature and Role of Plant Succession

Dynamic ecology concerns itself first and foremost with causes and processes and in consequence its dominant theme is one of change. The recognition of the basic fact of succession in vegetation has become more and more general in recent years, although at first it had been applied largely to local terrains such as dunes, bogs and swamps, with little recognition of their relation to the climax about them. As time has passed, however, an appreciation of the values to be obtained from a wider knowledge of the extent and character of the successive changes in the vegetative cover, has developed. As a consequence, federal agencies and large institutions have turned to intensive and extensive research into the subject, with results of the greatest practical importance to forestry, agriculture, range management and soil conservation.

Darwin once said that every traveler should be a botanist, since plants furnish the chief embellishment of all landscapes. Today it may be asserted with equal warrant that the traveler should be an ecologist if he is to understand the changes wrought by nature and by man upon the countenance of Mother Earth.

Even the everlasting hills are not ageless, for they are worn down by wind and water; lakes are filled, rivers grow old, and swamps become dry land subject to the plow. Intimately connected with these changes, hastening or retarding them, and in turn being modified by them, are the populations of living things, interacting in a maze of causes and effects of endless variety.

Most responsive of these is the plant cover, forming the pattern of a complex community in which animals and primitive man in particular find shelter and homes and from which they draw food and materials. Every such community is essentially an organism, of a higher order than an individual geranium, robin or chimpanzee, but possessing structure and development, and a coordination of functions and parts similar in many respects. Like them, it is a unified mechanism in which the whole is greater than the sum of its parts and hence it constitutes a new kind of organic being with novel properties.

Plant communities arise, grow, mature, attain old age and die from natural causes or by accident. They regularly reproduce themselves after partial destruction by fire, lumbering, clearing, or other disturbance, regenerating new parts, not altogether unlike the process by which a lobster grows a new claw or a lizard a tail. The final or adult community is termed a climax by reason of the fact that it is the highest type of social organism capable of growing in a particular climate, and its process of growth is known as succession, from the series of transient populations that pass across the scene.

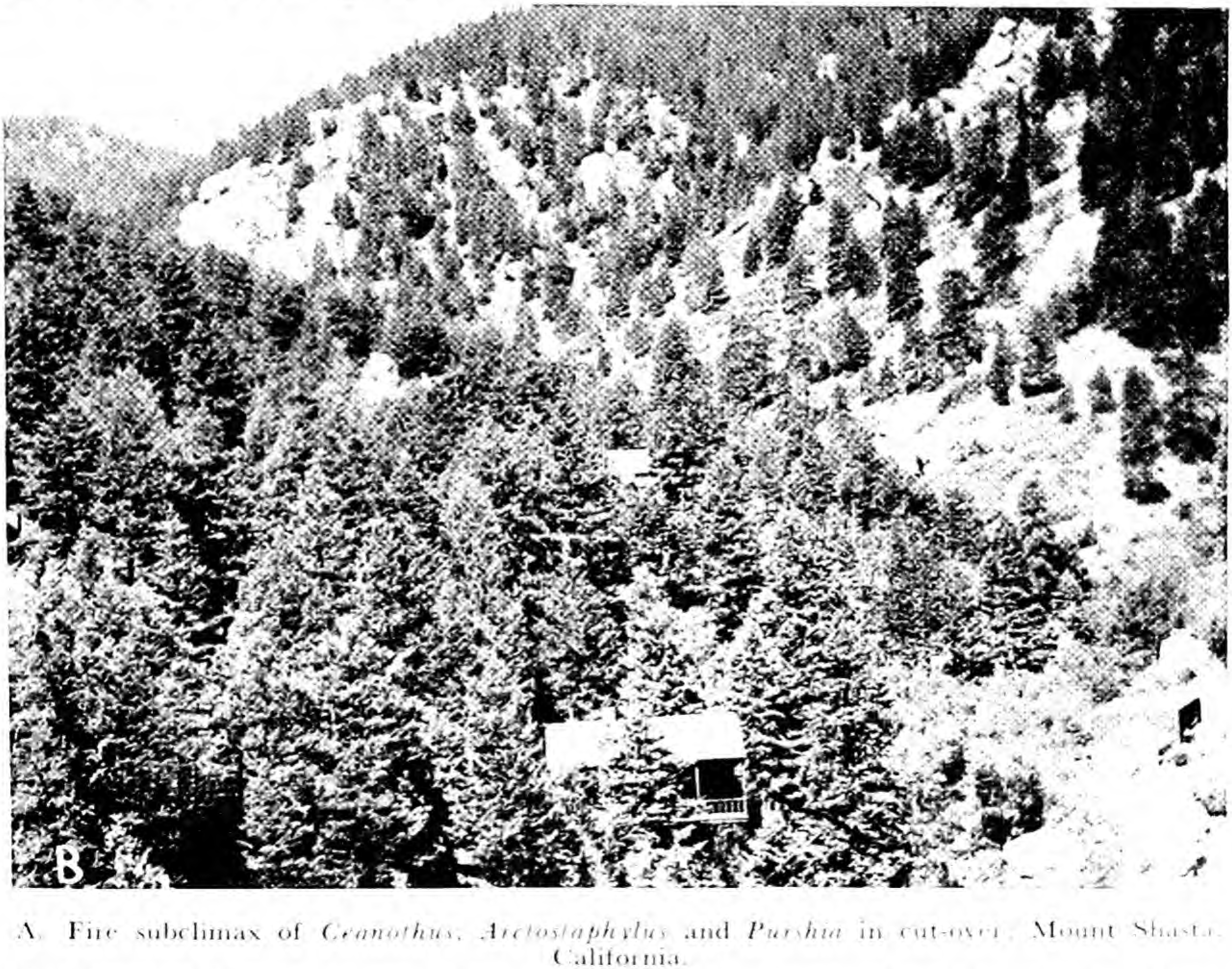
Plants Indicate Conditions.—The significant outcome of these relations is that both species and communities serve as measures or indexes of conditions and hence are known to the ecologist as indicators. In connection with land classification, agriculture, forestry, grazing, erosion, flooding and water supplies, the use of indicators furnishes a method of primary importance (Chapter III).

They indicate not merely the present features of climate and soil, but they also possess the clairvoyance of forecasting future changes and the possibility of controlling them, as well as of deciphering past events. Thus, climax and succession have not only great practical applications, but also provide the open sesame by which traveler or nature-lover may unlock the pages of nature's book and read the past and present of every landscape, and likewise its further story.

The primary indications have to do with climate and soil and the outstanding changes of the past, but woven into this pattern is the infinite variety wrought by man, directly through fire, settlement, logging, cultivation and so forth, or indirectly by grazing, erosion, flooding, draining. Each of these processes has its own indicator communities, and its major effects can be read with almost as much certainty as though recorded on the spot by an eye-witness (Plate 1A).

The Great Plant Climaxes.—Everyone is familiar in a general way with the great climaxes of our country and especially with the two most extensive, the eastern forest of beech, maple, chestnut and oaks, and the prairies of many kinds of grasses. In addition to these are the great transcontinental forest of spruce and fir to the northward and the Barren Grounds of sedge and lichen stretching along the Arctic Circle from ocean to ocean.

Related to these and hence of signal interest as seeming far out of place, are the alpine tundras of Mount Katahdin, Mount Washington,



A. Fire subclimax of *Ceanothus*, *Arctostaphylus* and *Purshia* in cut-over, Mount Shasta, California.

B. Climax of Douglas fir and yellow pine marking the climate of middle altitudes. Alpine Laboratory, Pikes Peak, Colorado.

and of Pikes Peak, Mount Whitney, Mount Rainier, and other high summits of the Rocky Mountains, Sierra Nevada, and the Cascades, all survivals of a distant time of glacial advance when the arctic tundra moved far to the south.

Each of these great communities consists of certain dominants, a ruling class drawn usually from trees or grasses and best fitted to the climate concerned, and of various subordinate groups, among which the flowering herbs of woodland and prairie are the most conspicuous and familiar. Each climax is the product of its particular climate and hence the indicator of it, and thus serves as the point of departure for all the disturbances brought about by man, and for all projects of utilization, restoration and rehabilitation under way or projected in the present national program (Plate 1B).

Kinds of Succession.—Examples of the growth of climaxes, of their childhood and adolescence are to be found everywhere within the corresponding climate. Most frequently seen are those due to disturbances caused by man, but others with a much longer life-span occur in pond and lakelet, on rocky ridge and cliff, in sand-dunes and badlands, on the exfoliating domes of Yosemite and in the sinter and diatom basins of Yellowstone geysers.

Wherever an area is bare or is denuded by natural agencies or by man and his animals, development begins, progressing slowly or rapidly in accordance as the site is water, rock or actual soil, and passing through a series of communities to end finally in the climax proper to each climate.

Primary successions on granite may require a thousand years or more between the pioneering crustlike lichens and the climax forest of oak or pine, and hundreds of years to fill a lakelet to the point where meadow or woodland can flourish on the humus soil. By contrast, secondary successions following fire or cultivation may take no more than a half-century for the complete cycle, and an abandoned field in the prairie may be reclaimed by the grasses in a decade or two.

Succession in Water.—Probably the most familiar kind of succession is that found in standing water, with its communities of pond-lilies, cattails, bulrushes and sedges. The pioneer colony of this series is founded by submerged stoneworts, pondweeds, hornworts and the like, in water up to about twenty feet.

As these grow and decay, the pond is gradually filled to the level at

which floating plants can push in and take possession. These then rule as conquerors for a while, but likewise bring about their own downfall by shallowing the water so that bulrushes, cat-tails, wild rice and reed-grass can invade usually in this order. The remains of these accumulate even more rapidly and in a few decades the pool may become a wet meadow covered with sedges, which in their turn yield to grasses and afterwards to shrubs, or in some cases to the latter directly (Plate 2B).

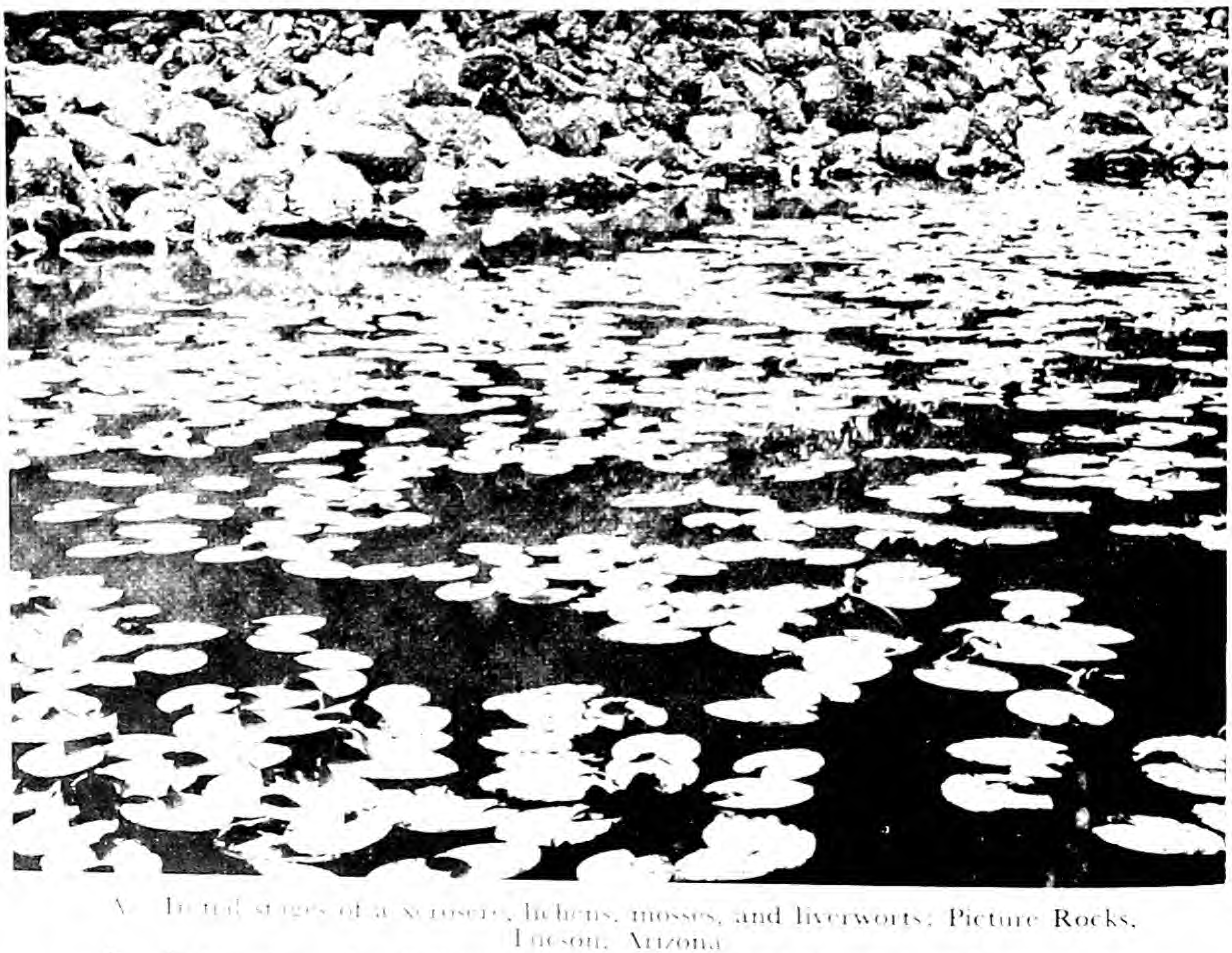
When the ruling caste of woody plants is once established in a forest climate, trees of small demands and rapid growth overshadow the shrub stage, and later yield to the invading phalanx of climax trees of slower growth but greater permanence. In the prairie region, the succession terminates with a community of drouth-resisting grasses, since the rainfall is not sufficient for the development to continue to forest.

Succession on Rock.—On rocky ridges, mountain peaks, lava fields and boulders everywhere, the course of succession is quite different. By contrast with water-plants, the chief task of the pioneers is to convert rock into soil and to increase the water rather than diminish it. In the miniature deserts of rock-surfaces only the humblest plants can thrive, such as lichens and mosses which are capable of enduring dessication for months.

The first settlers are crust-like lichens, which etch the surface and slowly produce a thin layer of dust. After many years, leafy species gradually invade and carry the task forward, yielding to mosses as a thin soil appears in crack and crevice. As the soil increases in depth, tiny saxifrages and other "rock-breaking" herbs enter, and these are followed after an interval by grasses. From this stage, the general course is the same as that in succession from water, inasmuch as grasses are followed by shrubs and these by trees in the case of a forest climate (Plate 2A).

Succession in Soils.—Succession on sand-dunes takes place more rapidly and dramatically since soil of a sort is already present and the major problem is to fix the shifting sand and enrich it with plant remains. To be a sand-binder, a plant must not only be well-anchored and hold sand, but it must also be able to catch the load borne by the wind and even more important, to keep its head above the sand as the latter heaps up about it (Plate 3A).

The early invaders are lowly annuals of small requirements, which gradually stabilize small areas for the entrance of an ascending series of perennials, either forbs or grasses. In the prairies, grasses of progressively



A. Initial stages of a xerosere, lichens, mosses, and liverworts; Picture Rocks, Tucson, Arizona.

B. Initial stage of a hydrosere, *Nymphaea polysepala*, in Two Ocean Lake, Yellowstone Park.

A

White Sands, Alamagordo, New Mexico.
A. Hummock of sand protected against blowing by *Rhus*.
B. Grasses and low shrubs forming early stages in succession on the dunes.

higher demands replace each other in forming a permanent cover, while in forest regions the grasses yield ultimately to shrubs and trees (Plate 3B).

The reconstruction of the adult community is a simpler and still more rapid process where fire or clearing has destroyed the climax. The soil usually is neither removed nor impaired, and in the case of fire is often enriched by the minerals liberated.

Mosses and liverworts appear almost at once, and during the first full season a complete cover of annual forbs and grasses may be formed. Many perennials and shrubs survive the fire and their root-sprouts soon appear in large number, gradually overtopping the herbs, reducing the light and taking the lion's share of the water in the soil (Plate 65).

The herbs are conquered by bushes and low shrubs; these are succeeded by taller shrubs, and trees then begin to straggle into the copses, or take more or less complete control by means of sprouts. After a few decades a young climax forest is again in possession.

A somewhat similar course is followed in cultivated fields that are allowed to "go back", the term itself indicating some popular appreciation of the process of succession. Annual weeds dominate for a few years, and the usual communities of perennials, grasses, and shrubs gain successively a short period of mastery, the return of forest or prairie often requiring but two or three decades.

Forces Concerned in Succession.—Succession depends for its opportunity upon the production of bare or denuded areas, but the driving force back of it is climate, each succeeding community becoming less controlled by soil or terrain and more by climatic factors until the adult stage or climax is attained.

The actual growth of the community is regulated by certain processes or functions by means of which soil and climate produce their effects. The initial processes are aggregation and migration, by which individuals are brought together to form communities. These react upon the soil and then upon the local climate to render conditions at first more favorable to themselves and later to the invaders that are to replace them, the actual conquest being brought about by the outcome of the competition for water, light, and minerals especially.

Within each community there is likewise a certain amount of cooperation, as seen in the reaction that produces shade, increases the organic

matter in the soil, minimizes the effect of wind, or augments the moisture of the air. The plants and animals of the community also exhibit many essential interactions, in some of which the mutual benefit is striking, as in the pollination of flowers by insects and humming-birds. When man enters the situation, such relations become much more varied and important, especially in the hunting, pastoral, and purely agricultural stages of human society.

Succession of Races and Cultures.—It is obvious that human communities are subject to the control of climate and soil—to what have often been called geographic influences. They exhabit aggregation and migration, reaction upon the environment and increasing control of it. Competition has been rife between and within them, and out of this has gradually emerged a new function, cooperation, first within the family and then spreading to larger and larger units under a slow but inevitable compulsion.

Succession has been less clearly perceived in human communities, though everywhere prevalent in prehistoric and ancient times, while modern rivalries disclose certain aspects of it. The first recorded succession is that of Chellean, Achulean, Mousterian, Solutrean and Magdalenian peoples in Europe, while the most complex has been the sequence of races in Mesopotamia, from Sumerian to Akkadian, Amorite, Babylonian, Assyrian, Chaldean, Persian, Macedonian, Mongol, Tartar and Turk.

Better known to us is the series of invasions that have swept over England, involving Pict, Goidel, Brython, Roman, Angle and Saxon, Dane and Norman. A similar succession on our own continent is illustrated by the Maya, Toltec, Aztec and the Spaniard in Mexico, by the various Pueblan cultures of the Southwest, and by the trapper, hunter, pioneer, homesteader, and urbanite in the Middle West (Plate 20A).

2. Application of Plant Succession to Human Needs

The applications of the principles of plant succession to human problems and natural industries are manifold. An outstanding instance of their practical importance is to be found in the litigation between Texas and Oklahoma over the location of the boundary formed by the Red River, in which millions of dollars in the Burkburnett oil-fields were involved. The decision of the United States Supreme Court in favor of

Texas was based upon the evidence obtained by application to the problem, of the principles of plant succession as laid down in 1916. The widespread use of these is exemplified in all the disturbances wrought by man in the vegetation of the globe, as is generally recognized in the case of fire and clearing. In addition, succession is invoked for its benefits in the rotation of crops, and it lies at the root of systems of forest management, and particularly of afforestation and reforestation. It is indispensable to land classification, and hence to regulated grazing and the utilization of the public domain. It is the chief tool in the control of run-off, erosion and floods, and the conservation of water-supplies for irrigation and urban use, as in the maintenance of all surface natural resources, including game.

The epic of the West has long celebrated the frontiersman ever pressing onward in the search for open spaces, and the pioneer treading on his heels in the unending quest for a home. It has sung of the conquest of nature, of heroism and success, and of the building of new commonwealths, but it has muted the themes of failure and tragedy, of unwitting destruction and unfulfilled hopes.

Clearing with the ax, turning the prairie sod with the plow, irrigating the valleys, and burning with no heed of the morrow, wave after wave of settlers has flung down the gauntlet to nature, caring little and knowing less of her resourceful and inexorable ways. The ebbing of one wave was lost to view in the advancing crest of the next, until the barrier of an inhospitable frontier was thought to have vanished forever.

Had the newcomers been skilled in reading nature's books, they would have met the hazards of successive frontiers more effectively or perhaps have refused the struggle against them. Among the many reasons for their failure to do either, perhaps none was so potent as the illusion, fostered alike by state, railway and speculator with lands to sell, that increased rainfall followed cultivation and that each disastrous drouth must perforce be the last. The processes of nature were to be reversed by the wishing-wand of man, and dry years were regarded merely as fleeting if unpleasant interludes in the westward march of empire.

Even less observant and intelligent was man in the face of his own destruction of capital in terms of land and cover, and the tragic consequences of his short-sightedness were minimized or ignored, until the salvation of the semi-arid regions could only be brought about from outside. Even at this, the task might have lagged endlessly had it not been for

the conjunction of drouth, dust-storm, and flood to a degree and on a scale never before known, but in direct proportion to man's destructiveness.

Basis for Accurate Prediction.—The solution of all problems that involve natural vegetation directly or indirectly, rests upon the fact that every plant or community is an indicator of the conditions about it and hence of the causes that lead to these. However, the judgment of many individuals, is more dependable than that of one and the verdict of many different kinds of plants grouped in a community is much better. In consequence, the study of the chief plant communities of a region affords the best measure of the climate and its possibilities, while the minor ones will reveal the significant variations of soil and topography.

When disturbance takes a hand, these primary indications may be greatly modified and the pattern becomes much more complex. Nevertheless, such mosaics can be disentangled by careful scrutiny, and the respective parts ascribed to climate, soil, or human interference. In a program of rehabilitation, the effects of the latter are of the most immediate importance, but they can be turned to account only as the indications of climate and terrain are understood and heeded.

Fortunately, plant communities not only reflect the controlling factors, but also the sequence in which changes occur, from which is derived their greatest value in human situations. They indicate not merely previous conditions and communities, but they also forecast what will happen in the future and hense serve as the basis for control of all kinds. In short, the plant cover on the ground is an epitome of past events and future possibilities, and the outcome of its manipulation by man, intentional or otherwise, can be predicted with much definiteness (Chapter III).

Changes in Practice Demanded.—From the foregoing, it is evident that plant communities as indicators furnish the most satisfactory method of determining the best use of the land. This is still true in spite of the fact that settlement throughout the West has demonstrated by trial and error what cannot be expected of the land in the various climates, but the outcome is still tinged with human optimism and befogged by the occurrence of wet and dry years. Between indicators on one hand and actual experience on the other, the facts are adequate to permit a classification upon the basis of proper use, though it must be realized that much farm experience runs to opinion rather than knowledge.

On such a basis, the belts of assured practice must be shifted east-

ward to the extent of several inches of rainfall, so that the grazing-forage industry occupies the western portion of the present farming region and the latter is restricted to the rainfall zone in which severe drouth and crop-failure come but once in a decade.

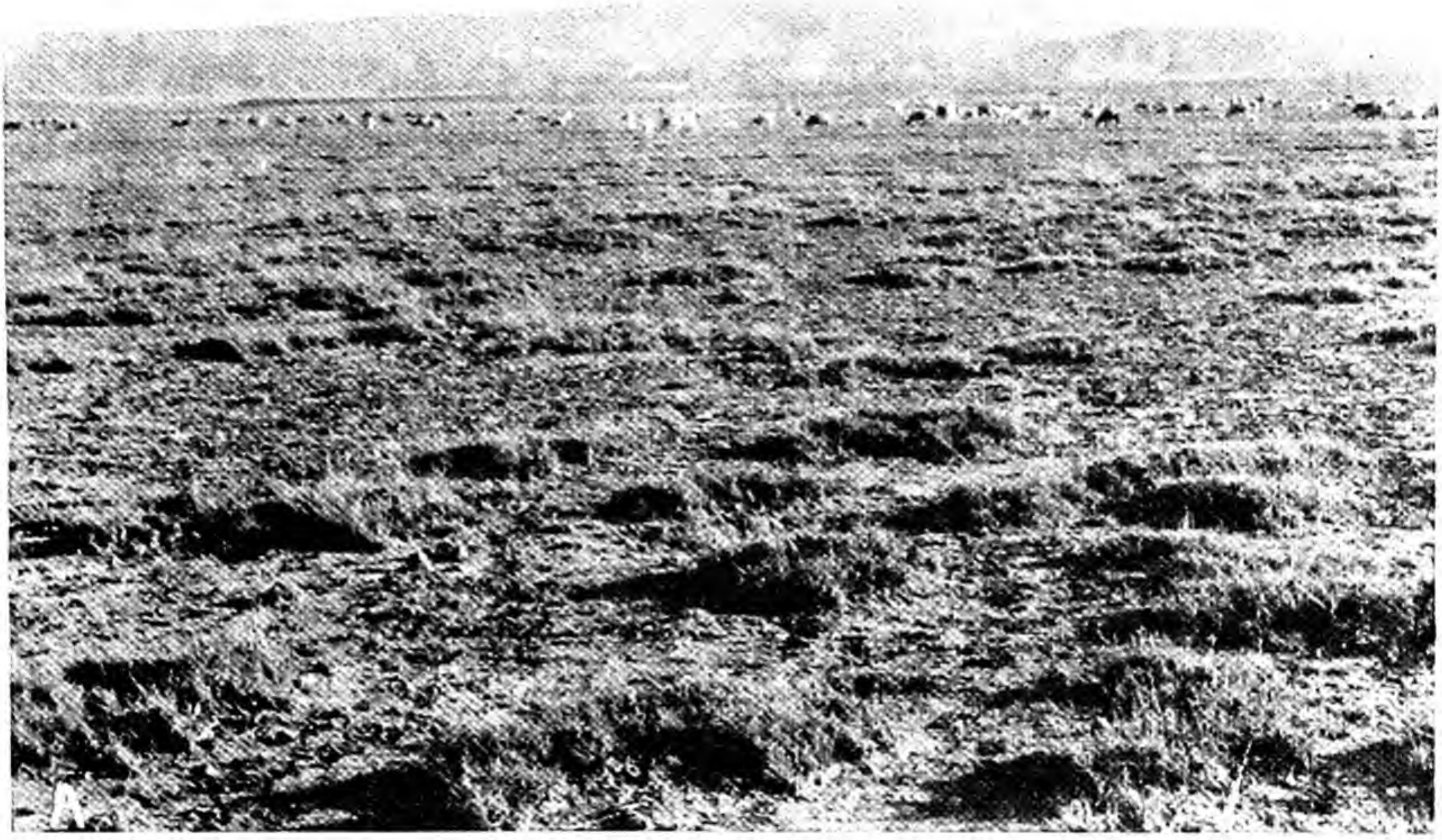
In addition, it must be fully recognized that millions of acres in the Great Basin and the Southwest should be withdrawn from their extra-hazardous use and reserved for their scenic or recreation values which are or may be relatively high. The vague terms "marginal" and "sub-marginal" should be dropped and all the lands of the West reorganized on the basis of regulated utilization grounded solely upon fact and not upon illusion.

The problems of forestry and grazing center about the maintenance of the natural climax, largely for the direct values in terms of lumber and forage, but increasingly also for the indirect ones, such as water-supplies, control of erosion and floods, and recreation in the widest sense. Conservation to secure similar objectives is a major concern of the national parks and of those state parks that are something more than picnic resorts.

On the other hand, agriculture and large-scale construction of various sorts rests upon the destruction of the native vegetation and are faced with the necessity for maintaining an artificial situation, at variance with the normal climatic and successional processes, as evidenced by the farmer's fight against weeds and by the fate of abandoned fields. Further evidence is furnished by the heavy toll taken by erosion, and the cure of the latter is to be found only in a field system that substitutes some other control for the natural cover or makes an approach to this in strip-cropping.

The wind-breaks of the shelter-belt project are likewise to be regarded as crops, but they are perennial woody ones, quite out of harmony with the climate and climax of the prairie and hence to be maintained against the grass dominants only by exceptionl means and in sites where soil or terrain is especially favorable.

Tragedy of Erosion and Flood.—While the drama of erosion reached its climax in the dust-storms of 1934 to 1936, the curtain had risen upon the scene with the advent of white men and the action had increased in tempo with each generation. Wherever the forest was burned or cleared, the prairie broken, the range overgrazed, or the cover destroyed by trails or roads, the protective role of plants was lost and the surface soil began to slip away, often imperceptibly but none the less steadily.



A. Navajo Indian Reservation range overgrazed by sheep near Gallup, New Mexico.

B. Gullies resulting from water eroding the denuded soil

Had the farmer of the Middle West been able to visualize the floods of the lower Mississippi or the contribution of his own land to the rapidly growing delta at its mouth, he might have been stirred to action. As it was, these problems were nobody's business but that of the engineer and he could cope with the damage only after it was done. He too failed signally to realize that dam and levee constituted but partial answers and that the adequate solution of the joint problems of erosion and flood lay in the control of watersheds.

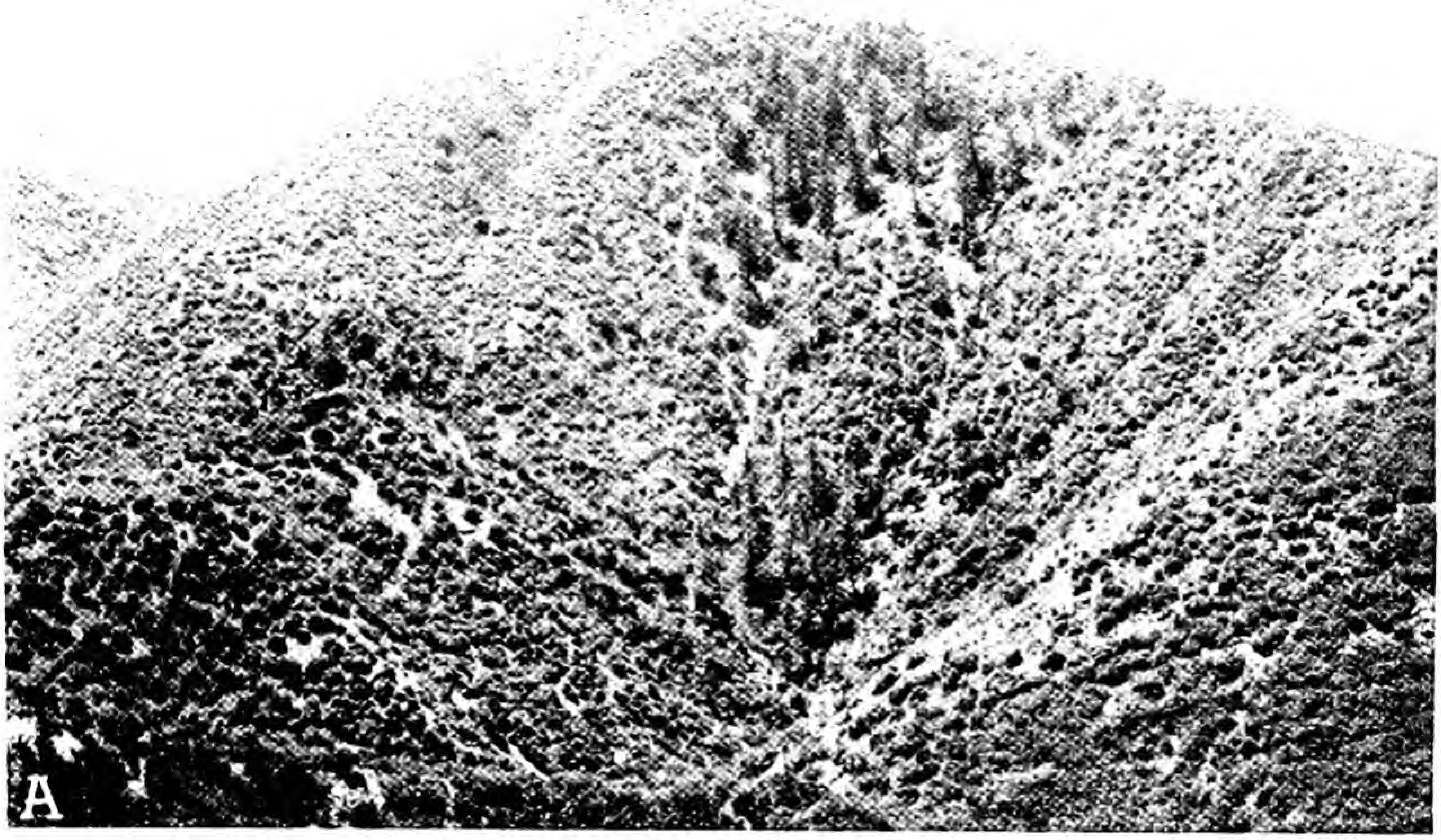
In short, these destructive processes are to be stopped before they begin on the head-waters of all the minor tributaries, a method that will at the same time salvage the fertile top-soil of farms and preserve the forage-value of grazing ranges (Plate 4).

The ecological principles involved in the connection between climate and climax and the effect of disturbance upon the latter are strikingly illustrated by tragic happenings in California in 1934. Fire above Montrose and La Crescenta denuded the steep mountain slopes of their protective cover of chaparral. A few months later, before the natural processes of recovery could act, a rainfall of 12 inches in 36 hours found nothing to impede its descent as a torrential flood, laden with destroying boulders. The towns at the foot of the mountains were overwhelmed and many lives lost, as well as homes and property destroyed (Plate 5).

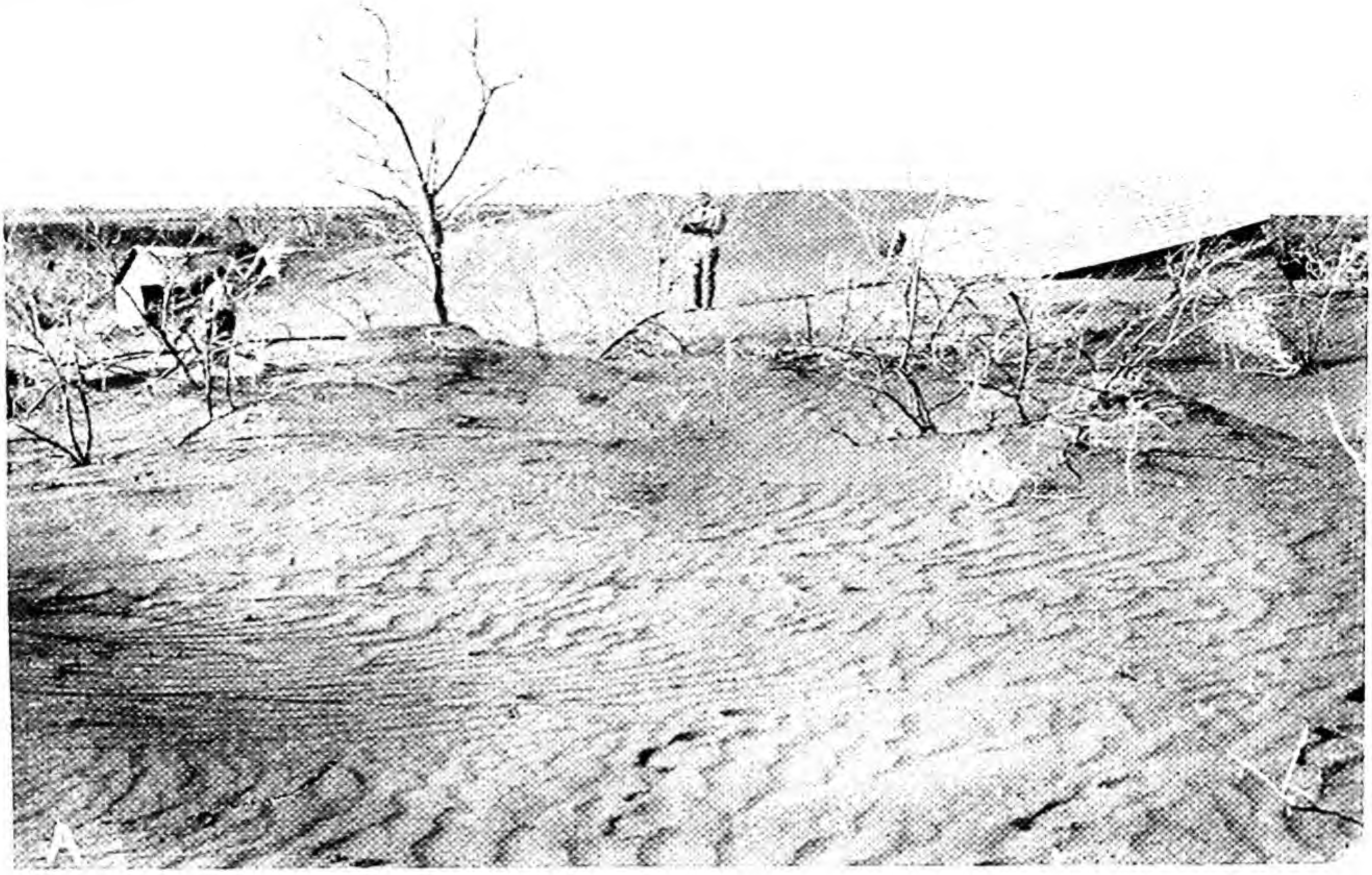
In May of 1935, a rain of high intensity falling on the badly overgrazed slopes of the Platte-Arkansas divide in Colorado wrought similar havoc in the valley levels of Colorado Springs. It destroyed every bridge for 300 miles along the Republican River and piled up flood waters to threaten metropolitan cities 600 miles away. This occurred in a climate and climax quite unlike those of southern California and arose from a wholly different kind of disturbance, yet the flood effects in terms of damage to property and loss of life were identical.

Better known because more novel, were the dust-storms of the summer of 1934 and the spring of 1935, marked by an intensity and extent never before seen in this country. Here again the primary cause was man's interference with natural processes, the widespread conversion of range lands into dry farms giving drouth and high winds their chance to turn the exposed soil into clouds of suffocating dust and to pile it over houses and barns in great dunes (Plates 6 and 60A).

The Problem of Recovery.—Just as a proper understanding of the role of disturbance would have prevented these calamities, in large part,



A. California mountain slopes protected against soil erosion by a thick cover of chaparral.
B. Site of garage and cottages swept away by the La Crescenta-Montrose flood caused by burning off the chaparral. California, 1934.



A. Dakota farmstead overwhelmed by dust storms during the drouth of 1935.
B. Fence buried by soil blown from adjacent ploughed fields; Burlington, Nebraska, 1935.

so must a realization of the inevitable relation between cause and effect be invoked to cure them, as well as to render them impossible in the future. Until fires can be wholly eliminated, every precaution must be taken to avoid the consequences that too often ensue. The factor of safety must receive every possible emphasis, all feasible steps must be taken to hasten the natural succession, and such adjuncts as debris basins and check dams must be so constructed as to play an assurred part (Plate 66).

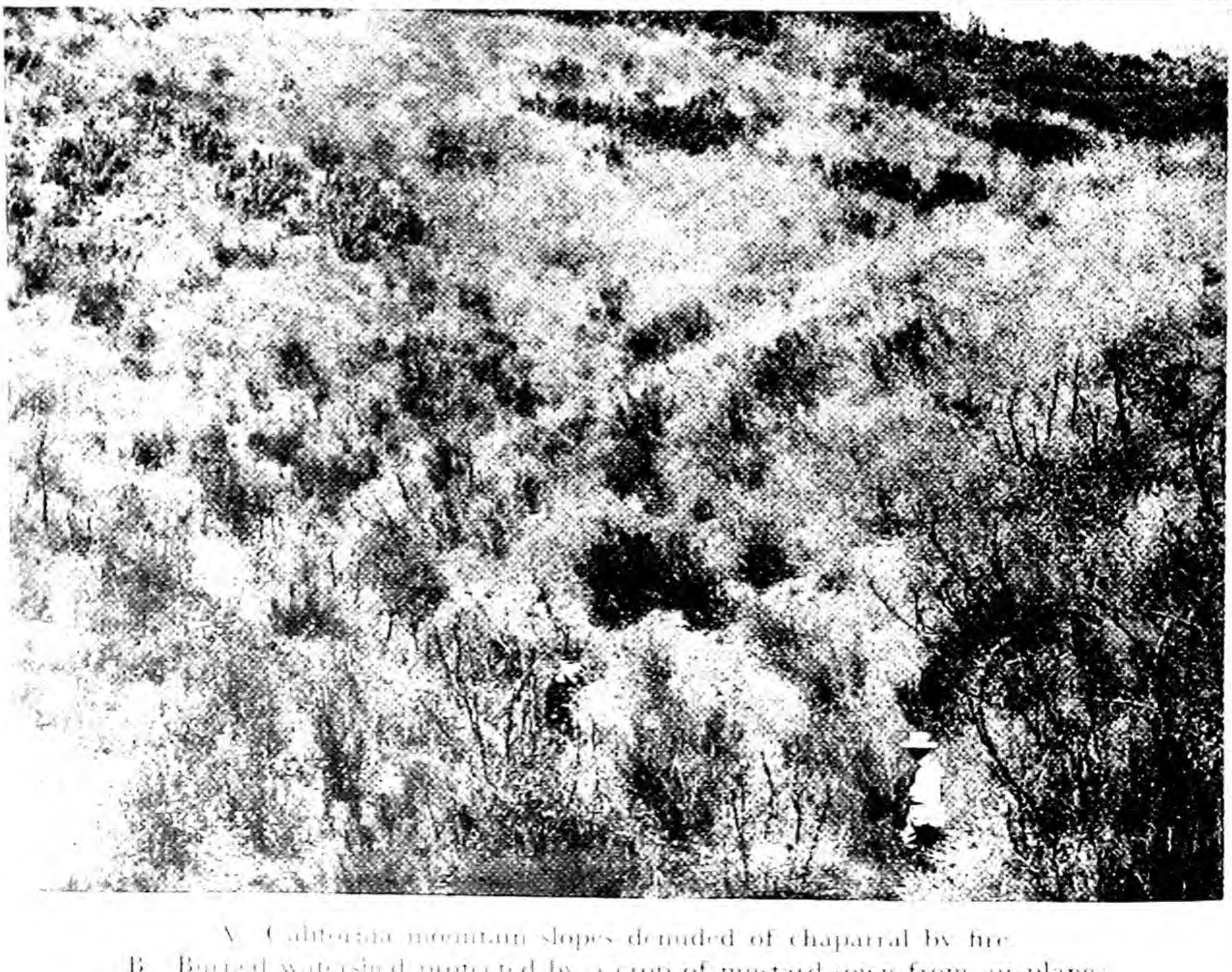
Since the early stages of succession have less effect in restraining runoff and erosion, it is essential to hasten the return of adequate control by means of artificial seeding. This has been done on a large scale over the burns at Montrose and Santa Barbara and with excellent results, the higher and steeper areas being sown from the air (Plate 7).

In the case of watersheds that have been seriously overgrazed, proper control of erosion and flooding can be secured only by removing all stock for a few years or by reducing the number to permit the recovery needed, together with such terracing and furrowing as the terrain demands. Here also restoration may be speeded up by sowing or planting, but the success of such measures depends largely upon the whims of the weather, as well as upon the kind of climate and climax.

The problem of recovery becomes much more difficult and complicated if the native cover is completely removed as a consequence of tillage. When the inevitable drouth enters such situations, the bare topsoil is whirled away in dust storms that may span the continent, or heaped into unsightly ridges, leaving a sterile waste in place of a farm (Plate 64A).

There is no adequate remedy for such a condition until the rains return and the weed seeds everywhere scattered by the billion, begin the task of succession to reclothe the soil. Although they perform this job well against both wind and water, once in possession, they can be displaced but slowly by the grasses. A quarter of a century may be required to reproduce the desired forage cover and it is imperative to employ an artificial succession under control that will restore the grasses in four or five years at the most.

Such a comprehensive attempt at rehabilitation has never before been attempted, but the body of facts concerning climax and succession clearly indicate the essential features of the plan. However, the chief problem is the human one, and it has already become clear that it is much simpler to formulate methods for desettlement and resettlement than



A. California mountain slopes denuded of chaparral by fire.
B. Burned watershed protected by a crop of mustard sown from air-plane; Santa Barbara, California.

to carry them out in the face of the habits and practices of a whole countryside.

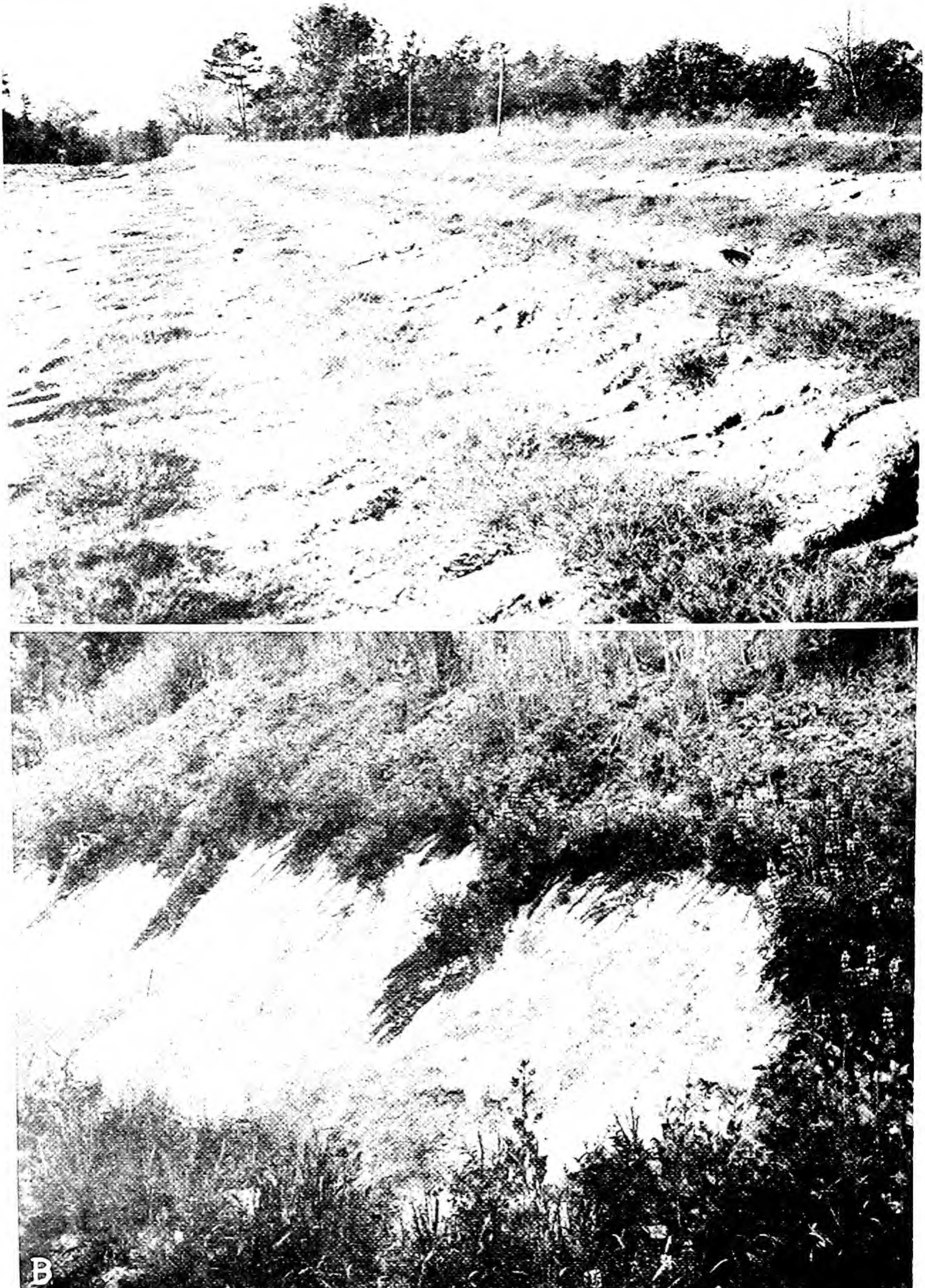
Precautions in Road Building.—By comparison with these staggering consequences to human welfare and survival, those that attend man's destructive acts in connection with road building and similar operations appear trivial. None the less, these may also exert serious effects in terms of safety in travel, as well as in devastating floods and mud-flows, to say nothing of costs of maintenance and repair. In addition, scenic values may often be destroyed or reduced in the very regions where they are greatest, as by the construction of main highways that steadily increase in depth of cut and height of fill.

Like all bare areas, the latter offer opportunity for the action of natural succession, but against the slowness of this must be set the certainty that the first heavy rain will cause serious and often catastrophic washing and slumping. To insure against this, effective methods have been devised for holding the loose soil by terracing and planting, imitating natural succession in some degree but assuring a protective cover the first year. The resulting succession is then controlled to produce in a few years the final pattern desired (Plates 8A, 68 and 69).

In most cases, if not in all, this should follow the principles of natural landscaping, which is characterized by employing native plants in harmony with the climax in general. It is as far removed as possible from the straight rows of streetside exotics too often regimented along highways, and rests squarely upon the major rule that well-ordered variety in materials, massing, color and texture is indispensable to the highest type of highway composition (Plates 8B and 70).

Nature's Cooperation Essential.—As an epilogue, it should be pointed out that nature's cooperation is essential to the success of the many present endeavors to undo man's destructiveness. Since this cannot be compelled, it must be won by understanding and insight. These have already been attained in fair measure with respect to climax communities, the process of succession, and the use of these as indicators of what has happened and can be made to happen.

But there is still to be achieved a much greater insight into nature's weather moods and the familiar but obscure chain of events known as climate. Practically all of the great projects now under way in the West would profit enormously by the ability to anticipate the more striking



A. Bermuda grass sodded on low terraces along the roadside; Texas.
B. Native vegetation gradually reclaiming bare slope; Santa Barbara, California.

fluctuations in rainfall especially, and it is in this direction that progress is most needed.

The first attempts to blaze the way to predictions made a year or more in advance have shown distinct promise. This is indicated by the fact that the use of rainfall records in conjunction with the sunspot cycle suggested the probability that the succession of dry years on the Pacific Coast would end in supra-normal precipitation during the season of 1934-35.

The same indexes also warranted the expectation of normal rainfall or better in the drouth region, after the unprecedented series of six dry years, and further indicated that the actual break would come about May first, and in harmony with the behavior of protracted drouths, should be signlized by downpours and floods.

Chapter II

COMPETITION IN PLANT SOCIETIES

(Photographs by J. E. Weaver)

1. Experiments in the Study of Competition

It is significant of the essential unity of living matter that the study of competition in plant societies should have received its impulse from the consideration of human populations and their food-supply. This theme is usually associated with the name of Malthus, who first gave it currency, but the central idea is to be credited to Franklin.

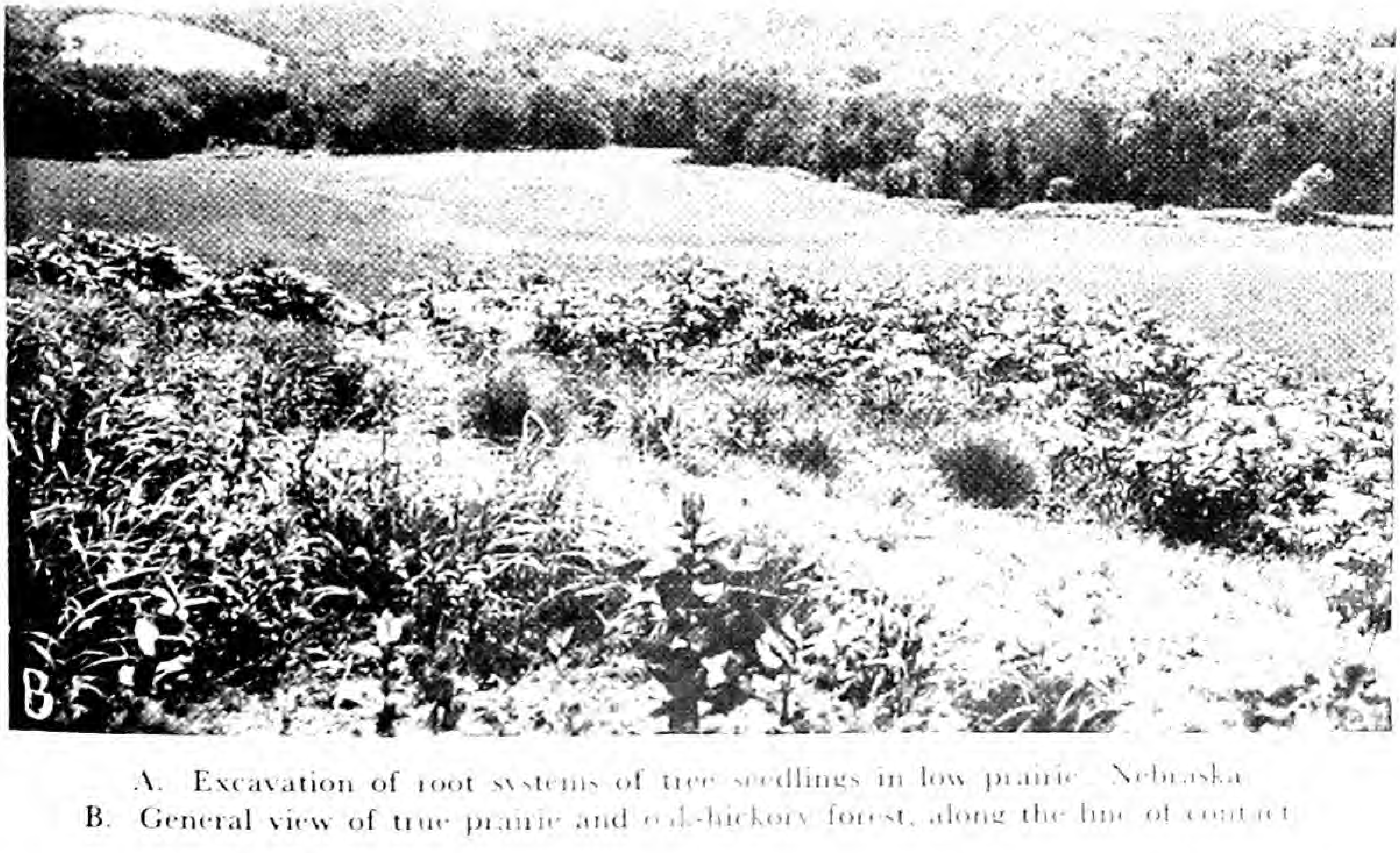
The progress of modern agriculture has deprived the assumptions of Malthus of anything more than historic interest, apart from the fact that Darwin found in them a basis for his theory of origin by descent. As he saw the struggle for existence, this furnished the mechanism by which the fittest survived, a process to which he gave the name of natural selection.

The tendency to geometrical increase in plants and animals and the limiting action of the food supply appeared so self-evident that Darwin felt no need to test this relation experimentally, though he did note that nearly half of the twenty species in a small plot perished as a result of competition. It was not until the rise of modern ecology with the methods of physics and chemistry at its command that an experimental attack upon this process became possible.

A Twofold Purpose.—The motives for this research were twofold. The first was to test the belief of Darwin that competition in nature led to the selection of the fittest individuals and consequent emphasis upon small but favorable variations, thus leading to the production of new species. The other was to trace the course of competition in societies and to discover its role in their development and behavior.

It seemed probable that this could be most readily accomplished by means of plant communities on account of their stationary nature. Plants possess the further advantage of manufacturing their own food-supply and hence are dependent upon the environment in a more direct and varied fashion than animals.

Quite aside from theoretical considerations, the century-long experience



A. Excavation of root systems of tree seedlings in low prairie, Nebraska.
B. General view of true prairie and oak-hickory forest, along the line of contact.

of gardeners and farmers had shown that crowding was unfavorable to the best growth of crops, and they had gradually evolved systems of sowing and planting that regulated density in such a manner as to secure the best yield. In spite of this, the details of the process and the role of the limiting factors were little or not at all understood, and these were to be revealed only through experiments designed expressly for the purpose. Hence, it became necessary to devise methods by which not only the behavior of the individuals could be studied, but likewise the qualities that spelled success or failure and the living conditions that proved decisive (Plate 9A).

To determine how general the process might be, it was further desirable to employ a variety of species through several years and to modify critically the environment in which they grew. This involved not only the use of crop plants, but also of native trees and grasses in such great natural communities as forest and prairie. These permitted the analysis of the two most important types of competition, namely, one in which the individuals were all of one kind, as in a clean field of wheat or corn, and another in which they belonged to two or more species, as in nature.

Additional Problems Investigated.—In addition to throwing light on Darwin's view of the origin of species and the succession of plant societies in their progress to the ultimate forest or prairie, competition experiments were expected to answer a number of everyday questions. Among these were the origin and nature of weeds, the meaning of "lime-loving" and "lime-fearing" plants, the weapons by which one species vanquishes another, and the course of the conflict where forest and prairie meet.

There was also the interesting problem whether plant societies, like human ones, enjoy "spheres of influence" quite outside the area actually occupied by them, whether crops exhaust the soil and hence are subject to the law of diminishing returns, and whether their roots excrete substances deleterious to themselves or to succeeding crops.

Furthermore it was hoped to disclose the effect of different seasons and climates upon the intensity and outcome of competition, and to evaluate the influence of animals, especially cattle and rodents, in the process.

While the weapons employed by plants against their competitors are innocent in guise, they lack nothing in effect. These are necessarily some feature of their structure, such as height of stem, size and spread of leaf or depth of root, or of behavior like quickness of germination and growth,

Competition between *Panicum* [illegible] and *S*[illegible]

A. Condition during the second season.

B. In the third season, *Solidago* gains the advantage over *Panicum* because of its greater resistance to drouth and winter cold.

resistence to drouth or frost, or to winter-killing. All of these confer a certain advantage in the struggle for water, minerals or sunlight, or in securing and maintaining possession against all comers (Plate 10).

Many Competitions Arranged.—The value of the equipment of each species is largely determined by the qualities of its competitors, a relation that can be determined only by actual test of their respective merits. For this purpose hundreds of contests have been staged between species of various life-forms, usually by pairs, to permit following the details of the struggle more closely. In this connection, it was needful to take a complete census of contestants at the outset and at regular intervals throughout the season, to measure their growth and survival and their final success in the production of finished materials, such as the seeds and underground stems that determine the number and vigor of the competitors for the next season.

Many hundreds of such competition cultures were installed in nature, in gardens and in greenhouse to permit varying degrees of control of conditions and of development. For crop-plants these contained a single variety as a rule, but in the case of native species, two were regularly paired. Some pairs were as evenly matched as possible, while in others one entrant was manifestly under a handicap (Plate 11). Tall grasses were matched against themselves or against short grasses, bunch grasses competed with those that form dense sods, annuals with perennials, and grasses were pitted against weeds, or trees or shrubs.

Grasses Dominant.—In general, the taller grasses enjoyed a decisive advantage over the shorter, but this was often counterbalanced by an earlier start or greater resistence to drouth or cold on the part of the latter. Not infrequently one species would acquire and hold the commanding position in the community and the other would perforce content itself with a subordinate role.

The fatalities were uniformly high, in imitation of similar conflicts in nature; an initial census of 500 might shrink to half that number by the end of the first summer, falling to two-score or so the second year, and reduced by the end of the third or fourth year to a bare handful of survivors.

When grasses were pitted against weeds, the latter practically always secured the initial advantage, owing chiefly to more rapid growth and the shading effect of broader leaves, best seen in the cultures with burdock and mullein. In the case of annuals, the weeds died at the end of sum-

Comparative growth of grasses in prairie and in denuded quadrat
A. *Stipa spartea* B. *Koeleria cristata*

mer and in spite of an abundant seed-crop, no new individuals appeared the next spring to dispute possession with the grasses.

With the biennial weeds, these usually maintained their ascendancy during the second season, but they too failed to leave any descendants to carry on the struggle. Even the perennial dandelion loses ground in competition with grasses, unless the latter are handicapped by mowing, as in lawns.

The complete possession finally secured by the grasses was due largely to the inability of the weed-seeds to germinate or the seedlings to survive under the conditions imposed by the grasses. The latter further possessed distinct advantages by virtue of their dense fibrous roots and vigorous offshoots. These facts explain why weeds cannot invade prairie or meadow unless the hold of the occupants is much disturbed and why they are usually at home only in roadsides, vacant lots and abandoned fields.

The Case of Buffalo Grasses.—A tradition still current in the Middle West holds that the prairies and plains were once carpeted by a dense turf of buffalo grasses and that these disappeared in the wake of the vanishing bison, presumably because of some vague bond of sympathy between the two! Another belief held that the tall bluestems had trailed westward after the pioneers and had filed on claims long before staked out by the short grasses.

Much field study had been given this problem in Nebraska and Kansas especially, before an opportunity offered to test the merits of tall and short grasses in actual competition. Within sight of the graceful obelisk of Nebraska's capitol was found a stretch of nearly pure buffalo grass, lagging half a century behind its departed namesake. Dotted through it were vestiges of tall grasses, apparently hopelessly discouraged by their diminutive antagonists. The area was fenced to demonstrate the part taken by grazing in this effect, and was charted annually for three years to trace the course of competition.

During the first season the tall grass recovered rapidly and produced seed for the first time. It increased its lead each year until it everywhere dominated the buffalo grass and had actually replaced it over much of the territory. In the weedy spots, a single year of protection restored the natural advantage of the grass to such an extent that the weeds disappeared as if by magic during the second summer.

Together with related studies, this experiment supplied the final link

of evidence necessary to explain the changes in grassland communities during the period of settlement.

When the bison roamed the plains by the million, they damaged the tall grasses more than their short competitors, giving the latter a decided advantage in the struggle and rendering them correspondingly dominant. As the buffalo were killed off or driven westward, the handicap to the tall grasses was removed in little more than a decade and these quickly assumed the rank allotted them by the character of the climate.

Similar experiments to redress the balance between the two kinds of grasses have been made throughout the West, always with the consequence of restoring the ability of the taller species to compete successfully with the shorter. The converse process is taking place in the tall grass prairies of the Missouri Valley, where confining cattle in pastures has had the effect of transmuting the bluestem community into buffalo-grass sod.

Struggle Between Forest and Prairie.—The present experiments in competition have proved to be of great value in throwing light upon the long-debated question of the origin of the prairies and their relation to forest.

Nearly every conceivable cause has been evoked to explain the distribution of these communities in the Middle-West, and it has been proved to the satisfaction of various proponents that the forests are advancing or retreating. The existence of groves, wood lots and orchards over much of the prairie region has led to the general assumption that trees will thrive naturally wherever they can be persuaded to grow artificially. But this view fails to reckon with the fact that, as in the case of man, the critical time in the life of a plant is infancy and that successful planting has not only demanded the removal of competitors, but also some direct aid through cultivating or watering.

While fire has often hindered trees in competition with grasses and has extended the sway of the latter by sweeping into marginal forests, the origin and migration of prairie have been primarily a consequence of favoring climate. As a result of the increasing heat and dryness following the last glacial retreat, a broad wedge of grassland was driven eastward deeply into the deciduous forest. At the advent of white men, this invasion had been flung back over a wide front through increasing rainfall, and, east of Illinois, isolated outposts alone remained to mark the farthest advance. The long persistence of such prairie openings in the forest is to be ascribed to the occupation exerted by the grasses and the handicap

placed upon the invasion of trees by their competition (Plate 9B).

Outcome of Experiments.—In order to reveal the detailed course of competition and the exact status of the present struggle between forest and prairie, several species of trees were planted in typical situations in meadow and upland in eastern Nebraska.

These were not species of high demands, such as the oaks, hickories, maples and beech of the eastern forests, but those of the forest rim, commonly employed for groves and windbreaks, like ash, elm, boxelder, and honey-locust. Both seeds and transplants were utilized, and the seedlings were given an initial advantage over the grasses in different ways and in several degrees.

In one series, the grasses were completely removed and the soil hoed from time to time; in another the grasses were clipped. The third series received water in times of drouth especially, while in the fourth no aid was given.

The general outcome was similar for all the species in the four sets of conditions, though some showed greater growth or survival for a time, owing to a more extensive or deeper root system. By the end of the four-year period of study, the survivors had been reduced to a tenth of the original number, in spite of the aid rendered, and all these were destined to succumb in a year or two.

When such shrubs as sumac and hazel were employed, the survival was naturally better by reason of their smaller demands, but even here the plants not artificially aided in competition with the grasses disappeared completely.

2. True Nature of Plant Competition

The operation of the law of supply and demand upon individuals of the same species was traced in crops of sunflower and of wheat by means of competition cultures with different degrees of crowding.

Sunflowers were especially favorable subjects because of their rapid growth and great size, and the corresponding demand for materials and energy. These were sown in six different plots of the same size, with the intervals between the plants decreasing from 64 inches through 32, 16, 8 and 4 to 2 inches. The growth of the stems and leaves was measured at periods of two weeks throughout the season, and the total production of dry matter and of flowers and seeds was determined at the end of the several series.

Competition cultures of field sunflowers.
A. 2-inch plot B. 64-inch plot

Effect of Crowding.—The supply of energy in terms of light and heat was roughly proportional to the square of the distance between individuals, while the amount of water and minerals was indicated approximately by the cube of this. As between plants of the same species, the chances of success were to be decided by more rapid growth, greater height, the number and size of leaves for food-making, and the depth and spread of roots in the soil.

A peculiar feature of the growth was the shifting of the maximum height from one plot to the next as each census was taken; at the outset the plants were tallest in the most crowded plot but soon lost the lead to the next, which was then overtopped by the third and so on.

By contrast, the rule of greater growth under less crowding was illustrated by stem diameter, which was but a fifth of an inch in the densest culture by comparison with 2 inches in the least dense. The equipment for manufacturing sugar ranged from 4 leaves in the crowded 2-inch plot to 28 in the open 64-in., and the total working area was 6 square inches in the one to 4,215 in the other, or nearly 30 square feet.

The average amount of dry matter produced in stem and leaves was less than one-tenth ounce in the one and a pound in the other. With respect to the final yield, the two extremes of density bore flower-heads respectively 1 and 8 inches across, the one weighing a fortieth of an ounce, the other 7.5 ounces.

The well-spaced individuals produced 1,803 seeds per head as against 15 for the crowded ones, and the weight per seed was seven times greater (Plates 12 and 13A).

Competition in Wheat.—The course of competition in wheat was followed in plots of four different densities, one representing the normal rate of sowing for crop production in the region and the others being one-half, twice and four times as much.

The response to crowding was even more consistent than in the case of the sunflower; the height and width of stem dropped rapidly from the half-normal to the 4-normal density, as did the length of leaf and the total leaf-area. The latter was twenty times larger per plant for the half-normal and the total production of straw equally great. There were four times as many heads per plant and these were nearly twice larger. In terms of yield per acre, the values were respectively 19, 21, 24, and 22 bushels, the maximum being in the plot with twice the normal rate of sowing.

A. *Helianthus*

B. Competition cultures of field

C. Yield of

This result was not unexpected and was largely due to the fact that the better yield per individual in the half-normal was offset in some degree by the much larger number of plants in the denser cultures. It also demonstrates a certain amount of cooperation between the individuals of a community, up to the point where the disadvantages of crowding become decisive, and suggests that the actual practice of farmers may be susceptible of improvement in this respect (Plate 13B and C).

New Methods Devised.—In the endeavor to penetrate more deeply into the true nature of competition, it became necessary to devise methods for the study of each limiting factor in turn, as well as to permit the analysis of the separate processes involved in growth and production.

Cultures of the same densities as in the field were grown in metal boxes to afford control of the supply of water, minerals and light in such manner that the amount of one of these would be limited in proportion to the number of plants, while the other two were compensated in accordance with the density. Competition between roots was eliminated in certain cases by planting individuals in metal cylinders, which could also be removed and weighed to measure the rate of water consumption. In other cultures the amount of light available as energy was varied by adding artificial leafy stems without the competition between the roots.

Since it was undesirable to remove individuals until full-grown, test-plants were installed at different levels from the base to the top of the culture to reveal the amount of water used and of starch stored at the different stages of growth in the several densities. Along with this went the study of absorption by the root-system, the pumping action of root-pressure, the rate of water conduction upward in the stems, the regulation of water-loss and gas exchange by the pores of the leaf, and the production of the finished materials.

The root-pressure was several times greater in the more open cultures, as well as in those in which the water of the soil was compensated in proportion to the crowding. Conduction in the stem was also twice to several times more active where the competition was least. A similar relation held likewise for the production of starch, which fell off regularly with increased density of individuals.

The breathing pores were particularly sensitive indexes of the intensity of competition, both in connection with crowding and the limiting effect of water. This was shown by variations in number and especially by the daily round of opening and closing, the period for gas exchange

and consequently food production being successively shortened as the density increased.

Things for Which Plants Compete.—As to the things for which plants compete, the results show that, in general, water is the most important. Light usually comes next, with minerals a close third, though the former permits a proportionally greater reduction before becoming critical.

This matter of the limiting factor varies more or less from species to species and especially as between native and cultivated plants. When the entire crop or most of it is removed from the field each year, minerals often assume the paramount role in competition. This is particularly true in long-settled regions with humid climate, where the amount of fertilizer needed is a fair measure of the relation between demand and supply. However, current views as to the exhaustion of the supply of minerals in the soil appear to be more or less incorrect, since the longest series of experiments known, 75 years of continuous cropping without rotation or fertilizer has failed to reduce the average yield.

Origin of Species.—The present studies in plant competition have clearly demonstrated that a limited supply of water or light will produce striking differences between individuals, not infrequently of the magnitude seen in varieties and species. This comes about in a single generation as a result of direct adaptation, but there is as yet no adequate proof that these new features can be fixed and hence transmitted to succeeding generations.

Furthermore, no experimental evidence has been obtained that the minute fluctuating variations emphasized by Darwin are accumulated year by year until they constitute a new species, and it now appears improbable that this is the case, in plants at least. Even in the prairie, where the stature and form of the grasses and forbs are the outcome of thousands of years of competition, it has proved possible to modify these greatly in a single year by removing individuals to the point where the supply is in excess of the demand.

Climax Communities.—These experiments have also served to confirm the view that the succession of plant populations, such as is exhibited in a burn, a sand-dune, the delta of a river or an old lava flow, is largely or wholly a consequence of competition.

Each successive community, from lowly moss or lichen to the final forest, owes its acquisition of territory and its "golden age" to the con-

quest of the original inhabitants, and will in its turn be dispossessed by more powerful invaders. The outcome of each period of competition is the dominance of the best-equipped community, until the incoming of prairie or forest puts an end to the waves of invasion and conquest, owing to the fact that each represents the highest type of population possible in the particular climate. This by no means indicates that competition is absent in these climax communities, but merely that the ruling class cannot be overthrown without a revolution. An accurate census of the prairie reveals the tendency for the brilliant flowers to be replaced by the dominant grasses, a fate that even overtakes the peas and clovers in spite of their service as nitrogen-fixers for the entire community.

Plant and Human Societies Compared.—Though the gap between plant and human societies with respect to competition seems a wide one, in the fundamentals of the process they exhibit much similarity.

The chief cause of difference between societies of plants and animals lies in the fact that plants compete for raw materials and energy to make food, and animals for a food-supply already manufactured. Furthermore, while many aquatic animals resemble plants in being fixed or sedentary, the majority are motile like man, and move about in search of food.

However, in essence, the similarities are greater than the differences, and a complete understanding of the nature and role of competition in society must rest upon the experimental study of the process in the whole range of social aggregations. In all of these, massing of individuals serves beneficial as well as harmful purposes, and the organization of the family group from the lowest to the highest organisms suggests the extent to which cooperation can be made to overrule competition.

The operation of the law of supply and demand is universal, from the simplest to the most specialized community, as likewise its corollary that competition is most intense between organisms or groups that make the same or similar demands. This often appears in the form of a struggle for space, but the actual contest is for the materials present or capable of being produced in it.

The visible effect of this is sometimes seen in the crowding out of stationary individuals, as in a row of radishes or a family of barnacles, but the essential competitive relation holds for the range of a pack of wolves or the hunting grounds of an Indian tribe. The final outcome is the occupancy or possession that constitutes the proverbial nine points of law, whether the society is fixed in one spot or is free to move about.

Competition Causes Migration.—Possession or domination as a result of successful competition is itself subject to the law of supply and demand, either through the increasing needs of a growing population or by changes, especially of climate, which decrease the available supply. The normal response to this is seen in migration, as a consequence of which the population pressure is diminished and the supply rendered more adequate for a time. This applies with peculiar force to communities of a single or similar species, but it holds also for the great complexes or climaxes composed of plants, animals and man, as is well illustrated by the mass invasions of late-glacial and post-glacial times.

The successive dispersions of the so-called Aryans from the steppes of southern Eurasia is to be most plausibly explained by the competition due to the crowding of a nomadic people, accentuated from time to time by the effect of protracted drouth-periods on their grazing ranges and consequently upon their food-supply.

In the peopling of our own West, climate was only an indirect factor, and the complex economic competition of a rapidly growing population was the primary cause of a movement ever westward in a search to redress the balance between needs and opportunity.

Chapter III

PLANT INDICATORS

1. Agricultural Indicators

General Relations.—Plants serve as indicators by virtue of their response to conditions about them. Every plant response has some significance, the kind and degree of which must be subjects of exact determination in each case. Some responses are obvious, others less evident, while still others are invisible though demonstrable. All these, however, must be referred to the habitat for the decision as to their meaning and their possible use as indicators. It is clear that the causal relation of the habitat to the plant is the primary basis of plant indicators. Each response is the effect of some factor or factor-complex acting as a cause, and is therefore the indication of this factor. As a consequence, it may also be employed to indicate the process or agency which causes or modifies the particular factor, as well as that in which the factor or habitat is involved. When the process is one set up or controlled by man, the plant likewise becomes an indicator of practice, and gives direct service in land classification, agriculture, grazing and forestry.

The relations of the plant or community to process and practice are direct corollaries of the basic principle that each is the best possible measure of the conditions under which it grows. Such measures require correlation with a particular process or practice to be of immediate service. This is the inevitable sequence, whether indicator values are the result of actual experience or the outcome of scientific investigation. In the latter case, the correlation is merely more detailed or more definite. Thus, while they all spring from the fundamental relation of plant or community to habitat, it appears desirable to distinguish indicators with respect to the use made of them. On this basis, they may be recognized as factor indicators, such as those of climate, light, temperature, soils, etc., process indicators such as fire, lumbering, cultivation, etc., and practice indicators of agriculture, forestry and grazing.

As the basic economic practice of plant and animal production, agriculture furnishes the standard for measuring the possibilities of soils, climates and regions. There are many reasons for this, chief among them the fact that it gives relatively large and immediate returns upon a small

capital. In addition, its operations are within the scope of the individual or family, and farming has become the traditional basis of the American homestead. The latter has played such a wonderful role in the development of the West that it has come to be regarded as a fetich, able to reclaim the most arid desert or to enrich the most sterile soil.

Land Classification

Nature.—The classification of land is an endeavor to forecast the type of utilization that will yield adequate or maximum returns. Properly, it should determine the optimum use as accurately as possible, and should insure the conditions under which development and utilization take place. In actual practice, classification has been conspicuously absent as a preliminary to the settlement of the arid regions of the West. Hurried and incomplete classifications have been made for special purposes, but these have covered only certain portions of the vast public domain and have usually suffered from inadequate and hasty methods. Perhaps their greatest fault has been that they were made with a particular end in view, and the primary object was to include or exclude as much land as possible without reference to its optimum utilization.

An accurate and unbiased classification of the land must necessarily take account of the enormous amount of scientific reconnaissance and investigation done in the West, during the last thirty years especially. It would rest upon a rapidly increasing fund of practical experience and experimental study of crops and methods, and upon the paramount importance of drouth periods and their recurrence in climatic cycles. In method, it would be complete, detailed, accurate, and unprejudiced, availing itself of all sources of information, but based primarily upon the relation of indicator vegetation to existing practice.

Relation to Practices.—While land classification is based primarily upon the division into agriculture, grazing and forestry, other considerations must also be taken into account. At the outset, it is particularly important that the future as well as the immediate present be considered. Many areas which are non-agricultural at present can be made available for crop production by the development of a supply of irrigation water or by draining the soil to remove the excess of alkali. On the other hand, the extension of agriculture into mountain regions on a considerable scale would threaten the water-supply of existing irrigation projects. The

maintenance of forests on a scientific basis is more than a present demand for lumber and fuel. It has a definite and often decisive bearing upon the agricultural possibilities of the land in the adjacent valleys and plains. Moreover, questions of reforestation and afforestation enter in relation to agriculture and grazing, and perhaps to climate also. While the use of land primarily for agriculture excludes forestry or grazing on any considerable scale, this is not true of the latter. Under proper safeguards, forestry and grazing can be combined in practically all forest and woodland areas, as is the case on the national forests.

The greater returns from agricultural land and the consequent possibility of supporting a larger population will always constitute a temptation to classify too much land as agricultural. If classification could be carried out only during drouth periods, this tendency would be corrected. On the other hand, it would be emphasized during wet years, such as 1915, when many regions received 50 to 100 per cent more than their normal rainfall. As a consequence, the classification of land as agricultural must be made with a definite knowledge of the existing conditions of rainfall and temperature and their relation to the usual variations of the climatic cycle. Moreover, it must be recognized that it is much less serious to classify a potential agricultural area as grazing or forest land than to classify the latter as agricultural. The former merely involves an insignificant economic waste until the real possibilities of the land become recognized, while the latter often results in recurring tragedies due to the attempt to make a livelihood where it is impossible. Hence, it should become a cardinal principle of land classification to rate as grazing or forest land all areas in which it is impossible to produce an average crop three years out of four. This would insure an adequate and permanent development of agriculture wherever possible and would warrant the introduction of scientific and economic systems of grazing, which would change it from a game of chance into an industry.

Proposed Bases of Classification.—While soil and climate have been employed in connection with various desultory attempts at classification, the only proposals which need to be considered here are those which deal with indicator vegetation. The latter necessarily takes account of both soil and climate and furnishes the only basis for an adequate system. Clements (1910) pointed out the difference between a classification survey and a use survey of occupied lands, and emphasized the necessity of using soil and climate, native vegetation and practical experience to

constitute a complete system for designating the lands of a region as agricultural, grazing and forest. A number of unoccupied townships of northern Minnesota were classified on this basis and several farming townships of the southern half were mapped in accordance with a use survey.

Use of Climax Indicators.—It is clear that the climaxes themselves furnish direct indications of great value for land classification. Thus, grassland, chaparral, and scrub are obviously indicators of grazing land, while forest and woodland are indicators of forest land. However, these comprise all the types, and a different method is necessary for the determination of agricultural land. This may be furnished by actual test, by the measurement of factors, or by the use of indicator correlations already established in other regions. As a matter of fact, some kind of farming test can be found almost anywhere in the West, in the driest deserts as well as at many altitudes. The studies of the last decade have made the application of indicator correlations almost universal, and the measurement of soil and climatic factors has at least been begun in practically every climax. As a consequence, it becomes a relatively simple matter to use climax communities to indicate those grazing and forest lands which are also agricultural, in that they yield a larger return from crop production than from grazing or forestry.

In the West, the climax which serves as the best indicator of crop production is naturally grassland. As the most extensive of all the formations concerned, its various associations serve also to indicate all the types of farming from humid and semi-arid on the east to dry-farming and irrigation farming in the west. While the alpine meadow climax has many points of resemblance to the grassland, it is a clear-cut indicator of grazing land, since neither trees nor crops can thrive in it. The various scrub climaxes, desert-scrub, and chaparral, as well as tree and scrub savanna, are primarily indicators of grazing land, unless irrigation is resorted to. Dry-farming is possible in certain areas in them, but these are usually in the transition to other formations or in the seral habitats. A notable exception occurs in the Coastal chaparral, in which the winter rainfall makes certain crops possible by evasion of the drouth period of summer. The woodland climax is primarily an indicator of combined forest and grazing land. It has some agricultural possibilities, but these are rarely to be realized except under irrigation. Of the three forest climaxes, the Coast forest is a distinct indicator of crop production

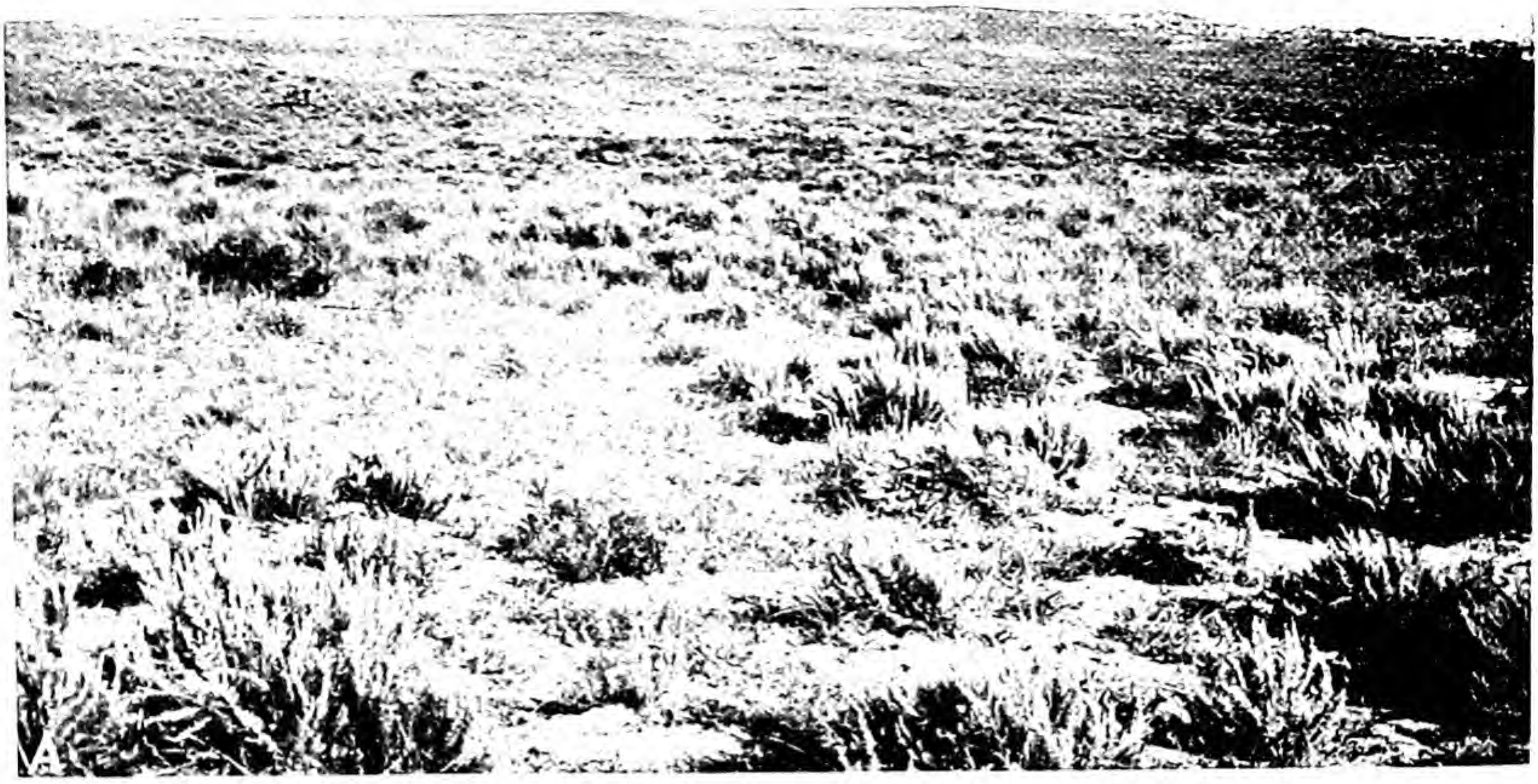
A. True prairie indicating agricultural land: Nebraska.
B. Oak chaparral and grass indicating grazing: Texas.
C. Aspen, spruce and pine indicating forest land: Colorado.

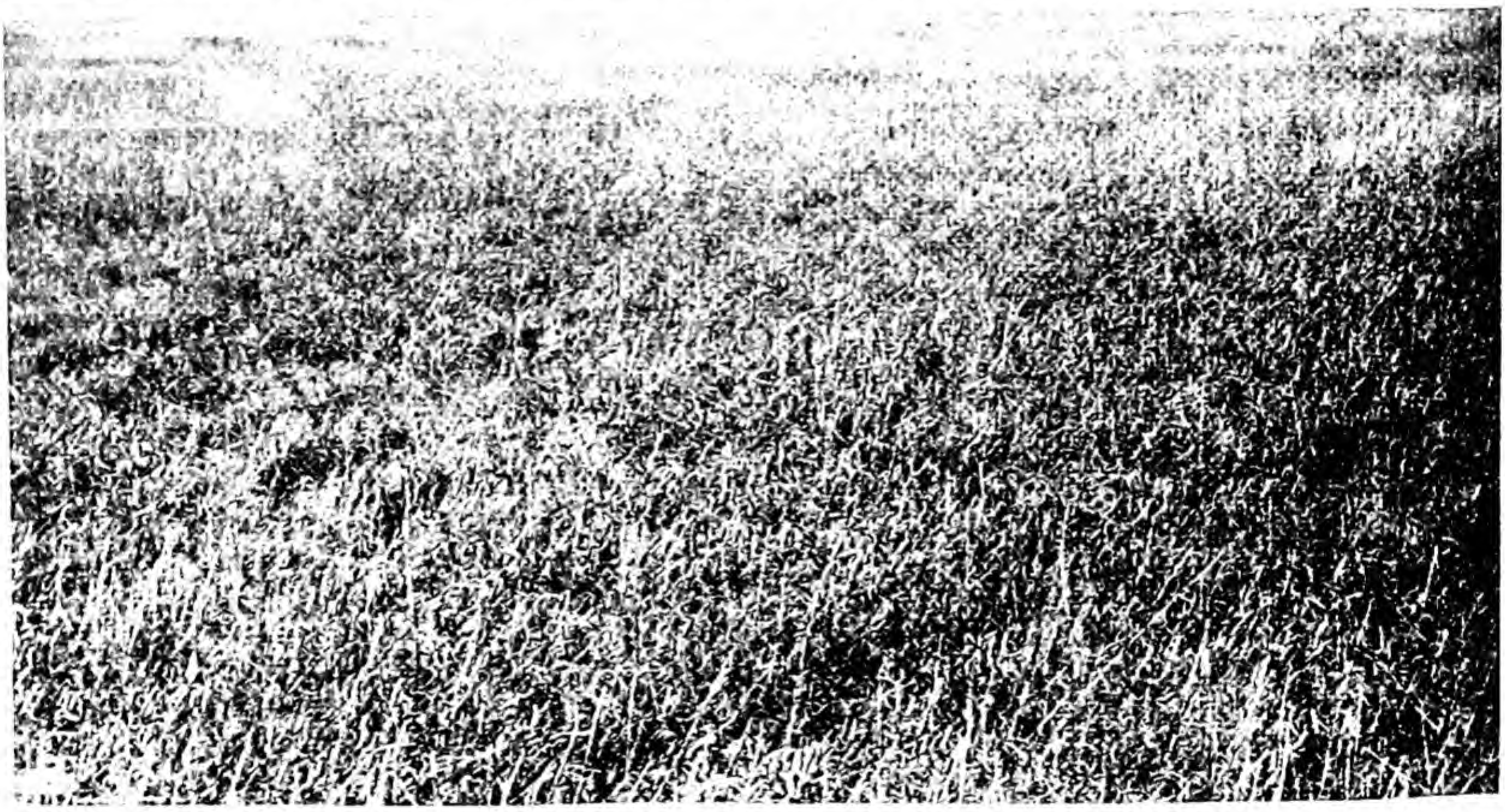
and the subalpine forest is just as clearly an indicator of non-agricultural land. The montane forest in general is like the subalpine in indicating forest-grazing land, but this depends upon the consociation and topography. The yellow pine consociation often indicates agricultural land, but the indication of the community must be checked by the nature of the topography and soil (Plate 14).

In the case of all climaxes, the relations of formation, association, consociation, and society to each other lie at the basis of the indicator correlations of the various communities. The indicator value of an association must be understood with reference to its formation, and that of the consociation with reference to its association. In general, these will be consistent with each other, and hence they serve to denote smaller and smaller areas, and particular crops and methods rather than types of practice. This is especially true of the many local groupings of dominants and subdominants. The societies formed by the latter are particularly sensitive indicators of local variations in climax conditions (Plate 15).

Soil Indicators.—The significance of soil indicators is local, as well as subordinate to that of climax or climatic indicators. The soil is especially important in the actual practice of land classification, since it is more tangible than climate and is subject to much greater local variations. Consequently in any particular region, climax indicators should be employed for general climatic values, while soil indicators should be used for the special values which will determine the proper classification of a particular area. In view of the paramount importance of water-content in arid and semi-arid regions, the general correspondence between rainfall and water-content from east to west becomes especially helpful. While texture and topography will cause soils to vary much locally in their water-content, the water-content of tillable soil decreases more or less steadily to the westward or southwestward.

The loess and glacial soils of the prairies are so completely cultivated that they hardly need consideration as to their indicators. The luxuriance of the three prairie associations and the large number of societies, especially of legumes, denote an agricultural region of the first importance. To the westward, the most extensive and important soils are gumbo or hard-land, saline soils, and sandy soils, usually of the sandhill or dune type. Where it is derived from the weathering of shales, as is frequently the case, the soil is usually both gumbo and saline. As Shantz (1911) has shown, hard-land is primarily agricultural in the Great Plains,





A. *Artemisia filifolia* indicating sandy soil; Canadian River, Texas.
B. *Bouteloua* and *Buchloe* on hard-land, Goodwell, Oklahoma.

though its high echard is a serious disadvantage during drouth periods. Soils recently derived from shales, such as the Pierre and the Graneros, however, bear a vegetation which suggests that their greatest value is for grazing. The work of Hilgard (1906) and of Kearney and his associates (1914) has shown that, in the Great Basin and similar saline regions, sagebrush is the one reliable indicator of agricultural land. While crops may be produced on land covered with *Atriplex confertifolia* or *Kochia*, it is only during years of exceptionally favorable rainfall, which are too rare for successful farming. Hence, practically all saline communities are indicators of grazing land, though such land may be converted to agricultural use when the removal of alkali is economically feasible.

The numerous sandhill and dune areas of the West bear distinctive indicators which denote the varying degree of fixation of the sand. Typically, they are grazing areas, though they are usually interrupted or surrounded by more stable areas, such as the wet valleys of the sandhills of central Nebraska or the wire-grass land of eastern Colorado, in which farming is possible. Even for grazing, their value is much less than it should be, and in addition there is rapid deterioration of the cover where overgrazing is practiced. There is no question that the grazing capacity could be greatly increased and the tendency to "blow" correspondingly decreased by protection and seeding or planting. The badlands which occur throughout the West, but especially in the Rocky Mountain region, likewise offer attractive districts for reclamation. Although the soil is hard clay instead of blow-sand and the erosion is due to water instead of wind, sandhills and badlands have much in common. The destruction due to erosion is often rapid and complete, as well as recurrent. They occur almost wholly in grazing communities, and the study of succession in both has reached a point where it is possible to make use of it as the chief method of reclamation as is shown in the section on "Grazing Indicators." The extremely dissected topography of badlands practically excludes agriculture, and in general the communities of rugged and rocky areas indicate their classification as grazing lands, even when climatic conditions might permit agriculture. In the case of swamp and bog communities, the direct indication is for grazing, but since they need drainage in order to be put into adequate commission, their classification should take this into account. When they are not too high or too far north, the drained areas will permit farming, but when they occur in the montane zone, or above, their chief value is for grazing.

A System of Land Classification

Bases.—As has been repeatedly emphasized, a system of land classification which is both practically and scientifically adequate must ignore no source of evidence. While indicator vegetation must be regarded as the chief tool, the latter is valueless unless it is correlated with practical experience and experiment on the one hand and with factor measurements on the other. Some indicator values can be disclosed by the use of a single one of these correlations, but all of them are necessary for complete certainty and accuracy. They not only serve to check each other, but also to reveal additional and final values. Furthermore, it must be recognized that all the climatic and hence many of the soil factors vary considerably and sometimes critically from year to year, and that this means a corresponding difference in crop production, and often in tillage methods. As a consequence, the annual variations in factors, indicators and production must always be taken into account and related, as far as possible, to an average or norm. The normal rainfall or mean temperature is insufficient for this purpose, especially since it fails to disclose the number and occurrence of the critical dry years. For this purpose the use of climatic cycles is necessary, and in consequence they must be assigned an important part in the classification of lands in arid and semi-arid regions. The existence and effect of such cycles are established beyond a doubt, and the chief task at present is to learn how to make the fullest possible use of them. This naturally depends upon the certainty and accuracy with which the dry and wet phases of the cycle can be predicted.

Classification and Use.—The close relationship between classification and use surveys and the importance of developing the one into the other can hardly be emphasized too strongly. The vital connection between the two in the proper development of the possibilities of the land may be seen from the following (Clements, 1910):

"The first step in determining the final possibilities of plant production is to ascertain just what the conditions of soil and climate are from the standpoint of the plant. This must be determined separately for the two great groups of lands, those still unoccupied and those now in use. For the former, a knowledge of soil and climate, and of the plant's relation to them is necessary to decide what primary crop, grain, forage, or forest is best. For the farms of the State, the best use is a matter of know-

ing the soil and climatic differences of regions and fields, and of taking advantage of this in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of different areas; to prevent the waste of human effort and happiness involved in trying to secure from the land what it can not give, and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it.

"A use survey is the logical outcome of the classification of land. Its greatest importance is with agricultural lands since grassland and forest permit less specialization in crop production. The period of the one-crop farm seems nearly closed; that of the special-crop farm is barely begun in this country. As a method of conservation, diversified farming is a permanent step in advance. It is the foundation upon which a distinctively successful country life is possible. But intensive cultivation is the open secret of scientific farming, and it demands the closest possible harmony between the plant machine, the raw materials which it uses, and the conditions under which it works. This makes possible the successful specialization of a region in a crop best adapted to the soil or climate more or less peculiar to it. The task of a use survey in this connection is to determine the special advantage of soil or climate, and to suggest the particular kind of plant machine and the method of production adapted to it. The same careful method of survey, which makes possible the best use of the different agricultural lands of the State, is likewise of great value on the individual farm, whenever differences of soil or exposure exist. The general nature of soil and climate of a farm must determine its special crop, and in a degree the secondary crops as well. But the complete success of the farm will rest upon a thorough knowledge of its differences of soil and climate, as well as upon a knowledge of the best varieties to grow or the best way to improve them."

Farming Indicators

Types of Farming.—With reference to indicators, types of farming may be based upon conditions or upon crops. Since the former determines the methods and return (and often the crop as well), it seems to afford the better basis. Accordingly, the usual division into humid and

arid farming is employed here, with a further division of the latter into dry farming and irrigation farming. It is clear that no sharp line exists between the types of agriculture in humid and arid regions. Between the two lies a broad belt of semi-arid country in which there is a gradual readjustment of methods and crops to increasingly arid conditions. The distinction is further obscured by the variation in rainfall from the wet to the dry phase of the climatic cycle. During the wet period, humid farming is possible through most or all of the arid belt and the need of drainage becomes felt over a much wider area. During the dry period, arid conditions are pushed across much of the semi-arid country and semi-arid conditions develop in the outlying humid areas. However, practices change much less than conditions; the general area of the humid, semi-arid, and arid regions remains essentially the same, with their mutual relations identical.

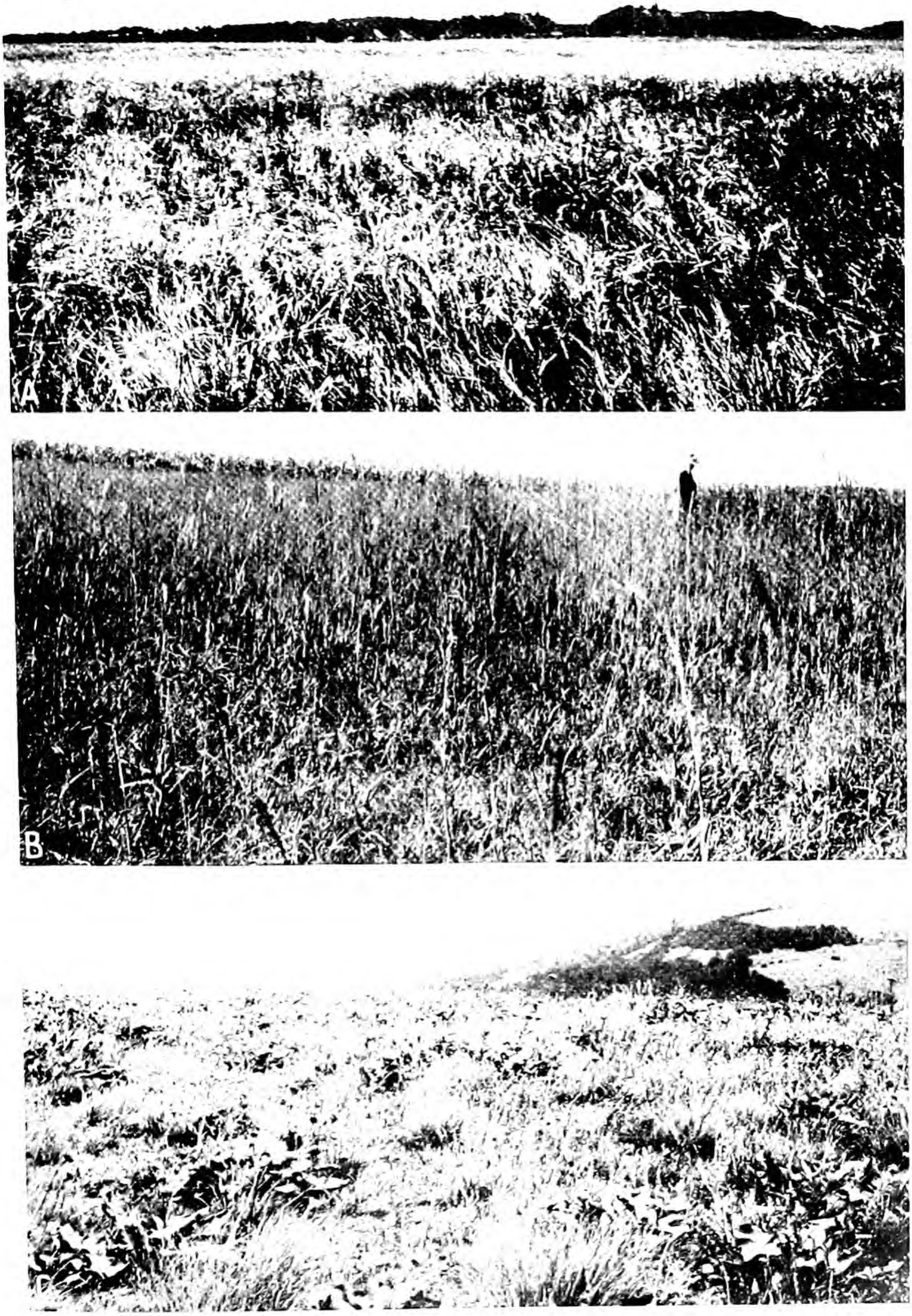
The humid region is regarded as possessing a lower limit of 25 inches of rainfall, while the semi-arid has a range of 15 to 25 inches, and the arid from 2 to 15 inches. As would be expected from variations in the annual amount and distribution of the rainfall, semi-arid areas with 20 to 25 inches of rain are characterized by the humid type of farming, and those with 15 to 20 inches by dry farming. The latter type usually reaches its lower limit at 12 inches, or at 10 inches where the rainfall is largely of the winter type. Below 10 inches, farming is profitable only by means of irrigation. Naturally, the latter is also extensively practiced in regions with 10 to 20 inches of rain, and to some degree under even higher rainfall. As Briggs and Belz (1911) have shown, the efficiency of rainfall depends upon the amount of evaporation, and hence decreases more or less regularly from the Northeast to the Southwest in the western United States.

Relation of Types of Farming to Indicators.—Because of the control made possible by irrigation, methods of tillage, and variation in crop or variety, indicator values are less definite in the case of types of farming than in grazing or forestry. Their significance is further reduced by the possibility of irrigation and by such economic considerations as markets and transportation. Moreover, the method of conserving water-content by means of summer fallow enables dry-farming to be practiced in regions where otherwise irrigation would be the only successful method. On the other hand, where annual cropping is the rule, dry-farming methods pass imperceptibly into ordinary farming with good tillage in

semi-arid and subhumid regions. In spite of this, there is a general correspondence between climax associations and types of farming. The tall grass prairies are typical of regions in which humid farming prevails. The mixed prairies and short grass plains denote country in which dry-farming of the annual crop type is more or less successful. The bunch grass prairies and desert plains characterize regions of scantier rainfall, for the most part of the winter type, and hence are chiefly to be correlated with dry-farming by means of summer fallow. Subclimax sagebrush has practically the same indicator value as the associated grasses. When these are tall grasses the indications are of dry-farming with annual cropping, and when they are bunch grasses they indicate summer fallow methods. Sagebrush is also an indicator of the latter when the rainfall does not fall below 10 inches. Over the major portion of the central Great Basin, sagebrush indicates a climate in which crop production is impossible without irrigation. This is likewise true of practically the whole desert scrub climax except for small areas at higher altitudes or near its eastern limit, where it approaches or mixes with the grassland. The indications of chaparral are variable. While they are largely non-agricultural, chaparral resembles scrub generally in its indication of dry farming or irrigation practices, as is true also of woodland where soil and topography are favorable. Montane forest usually receives enough rainfall to make humid farming possible, though both dry-farming and irrigation are practices in the lower yellow-pine belt. Most of the montane zone lies above the limit of profitable agriculture, and the occasional fields of hardy cereals are restricted to the warmer valleys and lower slopes (Plates 16 and 17).

Edaphic Indicators of Types of Farming.—These are more local and less important than the climatic indicators just discussed. They are primarily related to soil and water-content, and consequently are of the greatest service in regions with marked soil characteristics, such as sandhills, badlands, saline basins, or in river or lake valleys with relatively high water-content. The same farm may have lowland and upland areas, or may show considerable variations in soil with corresponding indications as to types of farming. This is particularly true of the wet valleys in the sandhills of Nebraska and of the many river valleys with a generally westward direction in Nebraska and Kansas. The wet valleys are marked by meadow communities and many of them are susceptible of farming by the usual methods. The river valleys are occupied by

A. Tall valley sagebrush indicating a deep soil for irrigation farming; Garland, Colorado.
B. A legume, *Lupinus plattensis*, indicating a rich moist soil; Monroe Cañon, Pine Ridge, Nebraska.
C. Relict *Stipa* and *Balsamorhiza* in sagebrush, indicating a bunch grass climate for dry-



A. Mixed prairie (*Stipa comata*) indicating dry-farming, Scenic, South Dakota.
B. Tall grass (*Andropogon furcatus*) indicating humid farming, Madison, Nebraska.
C. Bunch grass prairie (*Agropyrum-Festuca*) indicating dry-farming with winter rain-fall, The Dalles, Oregon.

similar communities of which *Andropogon, Agropyrum, Calamovilfa, Elymus* or *Spartina* are the dominants, or they may be characterized by the presence of scrub. In either case, the indications are for subhumid farming, especially during the wet period of the climatic cycle (Plate 17B).

Shantz (1911:85) has pointed out the agricultural significance of the difference between lighter and heavier soils in passing westward. The lighter soils conserve water to a much larger degree, and hence require less intensive methods of cultivation than do the heavier ones. In some regions, and especially during certain years, this may amount to ordinary cropping on one and dry-farming on the other. Kearney and others (1914:416) have shown that sagebrush (*Artemisia tridentata*) is an indicator of both dry-farming and irrigation farming in Utah when it makes a good stand and vigorous growth. Communities of *Kochia vestita* or *Atriplex confertifolia* generally indicate the necessity of irrigation to rid the soil of the excess of salts. The mixed community of *Sarcobatus* and *Atriplex* has essentially the same significance, though it indicates the desirability of drainage as well. Hilgard (1906:536) regards *Sporobolus airoides Spirostachys, Salicornia, Suaeda, Sarcobatus, Frankenia, Cressa,* and *Distichlis* as indicators of the necessity of underdrainage as a prerequisite to successful irrigation farming.

Crop Indicators

Nature and Kinds.—While the factor-complex must always be kept in mind in the correlation of indicator communities and crops, water is the paramount factor practically throughout the West. The importance of temperature as a direct factor increases with latitude and especially with altitude, but it is regularly less than that of water. The water relations are primarily a question of rainfall and evaporation, more or less modified locally by topography and soil. As a consequence, it is desirable to distinguish climatic and edaphic indicators of crops. The former denote the general climatic regions for particular kinds or varieties of crops, the latter the soil or topographic differences which break up the climatic uniformity of a particular region and render other kinds of varieties preferable. Climatic indicators are primarily climax communities of varying rank, while edaphic indicators are mostly seral or developmental communities. Crop indicators may serve to note (1) the type

of crop, as grain or forage; (2) the species in a general sense, as wheat, oats, or rye; (3) the kind, as winter and spring, or hard and soft wheat; and (4) the variety, such as Marquis, Fife or Preston. They also permit correlations with differences in methods of practice, such as dry-farming with and without summer tillage, etc.

Little use has been made of plant communities as indicators of the type or kind of crop. This has been a natural outcome of the enormous amount of crop experimentation carried on by the Department of Agriculture and the various State experiment stations. Nearly 100 stations and substations have been concerned in this work, and it is a logical conclusion that they have made the use of crop indicators unnecessary. It seems, however, that the very extent and thoroughness of the experiments with various crops must increase the accuracy and readiness with which indicaors can be used. In spite of the numerous stations, there are many large regions still unrepresented. In addition, the climatic gradations and edaphic variations are so numerous that the native vegetation alone affords an adequate method of taking them all into account. As a consequence, the opportunity for working out a general system of crop indicators seems exceptionally good. This would be based upon the correlations between native communities found about each station and the types and kinds of crops demonstrated to be the most desirable for that region. While such correlations can be obtained from the results of practically all stations, the investigations carried on at those of the Office of Dry-Land Agriculture are of the greatest value. This is due to a number of reasons, chief among which are the use of the same crop and methods, the wide extent of the studies, the large number of stations in a single great climax, the grassland, the more or less gradual decrease in rainfall to the westward, and the consequent readiness and accuracy with which comparative results can be obtained. The correlations discussed below have been based chiefly upon results obtained by this Office, supplemented for the more or less representative central portion by the studies made at the experiment stations of Nebraska and Kansas. In all of them, it should be borne in mind that the correlation and the corresponding indicator community have the greatest accuracy in the region of the particular station or stations, and that this value decreases more or less regularly in the direction of stations with different correlations. However, the practical usefulness of the indicator increases with the remoteness from a particular station, providing always that the plant community

remains the same, since the latter indicates that the conditions are essentially unchanged.

Climatic Indicators of the Types of Crops.—The correlations considered here are based upon the fact that crops, like natural dominants, have an area of maximum production about which they shade out in all directions. This diminution is generally less marked in the case of crops, owing to the modifying influence of culture as well as of economic factors. Corn affords the most striking example of a crop grown throughout an extensive region, but with a well-defined area of maximum production. As a crop it extends over the major portion of several climaxes, but its optimum area, the "corn belt," is more or less clearly limited. The limits of this belt fall within the main area of the subclimax and true prairies, which are to be regarded as the indicators of maximum corn production. In this connection, it is at least suggestive that four of the dominants of these communities belong to the genus *Andropogon* which systematically and ecologically resembles corn more closely than do any of the other grassland dominants. As might be expected, wheat exhibits an even more extensive correlation with the grassland. The region of maximum production is from Saskatchewan to Oklahoma, with secondary maxima in Indiana and Illinois, and in Washington and Oregon. The maximum falls almost wholly within the region occupied by the true and mixed prairies. Here also it is perhaps significant that *Agropyrum,* with its close relationship to *Triticum,* is an important dominant in these communities and is the major dominant in the great wheat region of the Palouse. Oats show a somewhat similar relation to grassland, as does barley, but rye manifests no clear correlation. On the whole, however, there is good evidence for regarding grassland made up of tall grasses as the primary indicator for the optimum production of cereals.

Hay and forage crops are more or less evenly distributed through the deciduous forest and grassland climaxes, but there is a clear regional differentiation in the case of alfalfa and sorghums. The chief center for alfalfa is in central Nebraska, Kansas and Oklahoma, with local centers in the main irrigated sections of the West, practically all of which occur in grassland or sagebrush. The sorghums, whether grown exclusively for fodder or for grain as well, have their center of production in western Kansas, Oklahoma, Texas and eastern New Mexico. It corresponds closely with the eastern half of the short grass associes, in which *Buchloe* and *Bouteloua gracilis* are the dominants. Cotton reaches its maximum

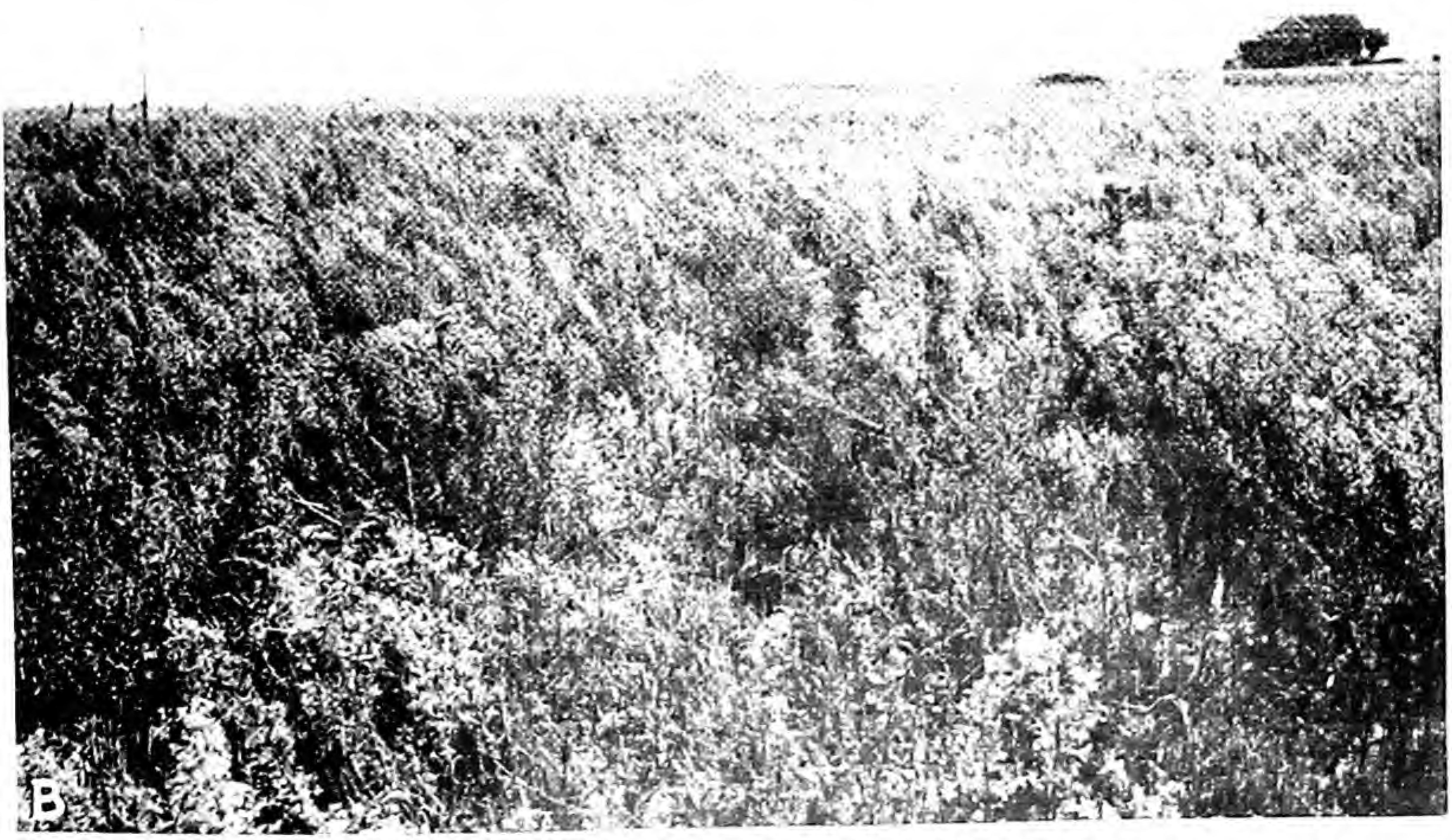
in a well-marked region which corresponds with the southern forest, except in western and central Texas and Oklahoma. Under irrigation it promises to develop a secondary center for long-staple varieties in the desert scrub climax of the Southwest. Of the other types of crops, vegetables are more or less evenly distributed over the eastern half of the country, with marked regional differentiation for certain kinds and many local foci. Fruits and nuts show a similar uniform distribution in the East, but they are almost wholly confined to the forested region and its extension into the southeastern prairies. This correlation is wholly to be expected on the basis of similarity in life-form. The most important fruit districts of the West lie in the sagebrush and grassland climaxes and depend upon irrigation, as the difference in the life-forms indicates.

Climatic Indicators of Kinds of Crops.—The correlation of the kind of crop with indicator communities has already been touched upon. It is often less definite than with types of crops, but there are a number of correspondences of much interest and value. These are perhaps best shown by the three kinds of wheat, namely, winter, spring, and durum. Winter wheat has its center in the true prairies of Kansas and Nebraska, in which *Andropogon* plays an important part. Spring wheat and durum reach their best development in the mixed prairies or in the northern portion of the true prairies, where *Stipa spartea* and *Agropyrum smithi* are especially important. They are more or less equal in value in the eastern portion of the true prairies, but durum shows an increasing advantage to the west, and is superior to spring wheat practically throughout the mixed prairies. In the bunch grass prairies of the Northwest the advantage is reversed, and spring wheat outyields durum. The general use of summer tillage in connection with the winter precipitation favors winter wheat because of its earlier period of growth.

The region of the maximum production of barley comprises the northern half of the true prairies, while that of oats includes the major portion of both the subclimax and true prairies. Flax finds its maximum in the transition from the true to the mixed prairies, but it is extending more and more into the latter in western North Dakota. While there is a marked correlation between the sorghums as a group, and the mixed prairie and their transition to the tall grasses, the various kinds of sorghums show no clear correlations with indicator communities. This is perhaps due in some measure to the relatively short period of trial, but probably results chiefly from the fact that qualities of earliness and dwarfness are more

significant than the group differences. In contrast with the grain-sorghums, the sorgos show an increasing correlation with the tall grasses, and in western Nebraska and the Dakotas are to be related to the mixed prairies.

Edaphic Indicators of Crops and Methods.—Variation in crop possibilities within a climate, due to edaphic or soil conditions, may be regional or local. Regional and local variations are both caused chiefly by variations in water-content arising from differences in soil, solutes or topography, and the only important difference between them is that the one determines the general agricultural practices of a region, and the other that of a neighborhood or of a single farm. The responses of plants to local differences in water-content are readily seen, and the corresponding edaphic indicators are of much value in suggesting desirable or necessary local variations in crops or methods. Since practically all such local differences have to do with water-content or temperature, their indicators have the same general significance as in the case of the more general climatic differences. Such local variations in conditions may often be quite as great as those between adjacent climatic regions and edaphic indicators may consequently denote differences in crops and methods quite as great as climatic ones do. Since the number of such indicators is legion, and every small difference of soil or topography has a corresponding indicator, the adjustment of crop and method to any particular variation in conditions is largely a matter of practicability. Locally as well as generally, the chief differences in soil are represented by saline soil, hard land or gumbo, and sand. All of these have their proper indicators, as is well known, and it is only necessary to recognize that their local occurrence has much the same significance assigned to them by Hilgard, Shantz, Kearney and others for more extensive regions. This is particularly well illustrated in the case of dune-sands, which are found in sandhill areas through the prairies and plains. It is best seen in the great sandhill region of Nebraska, where soil and topography have combined to present an unusual set of conditions. The loose sandy soil, lack of humus, and the maze of steep hills with intervening wet and dry valleys constitute a complex of factors marked by distinctive indicators and demanding a specialized type of agriculture. Such a region not only requires different methods and crops from those of the general climatic area, but the varying areas of wet valleys, dry valleys, and hillsides demand corresponding differences in treatment.



A. Ruderal crop of Russian thistle (*Salsola*) in a field of feterita, Dalhart, Texas.
B. Ruderal crop of horseweed (*Erigeron canadensis*) in a fallow field, Goodwell, Oklahoma.

Indicators of Native or Ruderal Forage Crops.—The detailed study of secondary seres in fallow fields and similar disturbed areas has revealed a number of species of native herbs and weeds which give more or less promise as forage crops. During the three years of drouth from 1916 to 1918, particular attention has been directed to those which made a vigorous growth or a good stand in fields in which forage crops were a failure, or in areas adjacent to such crops. A considerable number of weeds of much promise has been observed over an extensive region, and in addition a number of native species has been suggested as of possible forage value by their behavior during drouth. By far the most valuable are *Melilotus alba, Helianthus annuus,* and *Salsola kali.* The former has taken its place as a forage crop in some regions and there seems little doubt that it will ultimately be grown as a dry crop over a wide area. *Helianthus annuus* has but recently been tested under field conditions, but the results agree with the evidence in nature to the effect that it is of much value in dry regions, and especially during drouth years. *Salsola* has been grown scarcely at all as a crop, but it has been cut as a weed crop and utilized as hay of a fair quality at least. While its tonnage is less than that of sunflower, it will often grow luxuriantly in places where the latter will not. This is true also of *Helianthus petiolaris,* which may be regarded as a dwarf native form of the common sunflower. The other coarse weeds whose behavior indicates that they will be found to have some forage value are *Chenopodium album, Amaranthus retroflexus, A. hybridus, Erigeron canadensis, Iva xanthifolia, I. axilaris* and *Brassica nigra.* The native species of weedy habit and of such vigorous growth as to suggest the probability of forage value are *Amaranthus palmeri, A. powelli, A. torreyi, A. wrighti, A. fimbriatus, Acnida tamariscina, Psoralea lancelata, Franseria tenuifolia, F. discolor, Atriplex rosea, A. expansa, Corispermum hyssopifolium,* and *Cycloloma platyphyllum.* The last four are adapted to saline soils, and the last two to sandhill areas as well (Plate 18).

2. Forest Indicators

Nature.—Forest indicators are of three chief types, namely, (1) those that have to do with existing forests; (2) those that indicate former forests; (3) those that indicate the possibility of establishing new forests. A community of trees is axiomatically an indicator of forest, but it carries

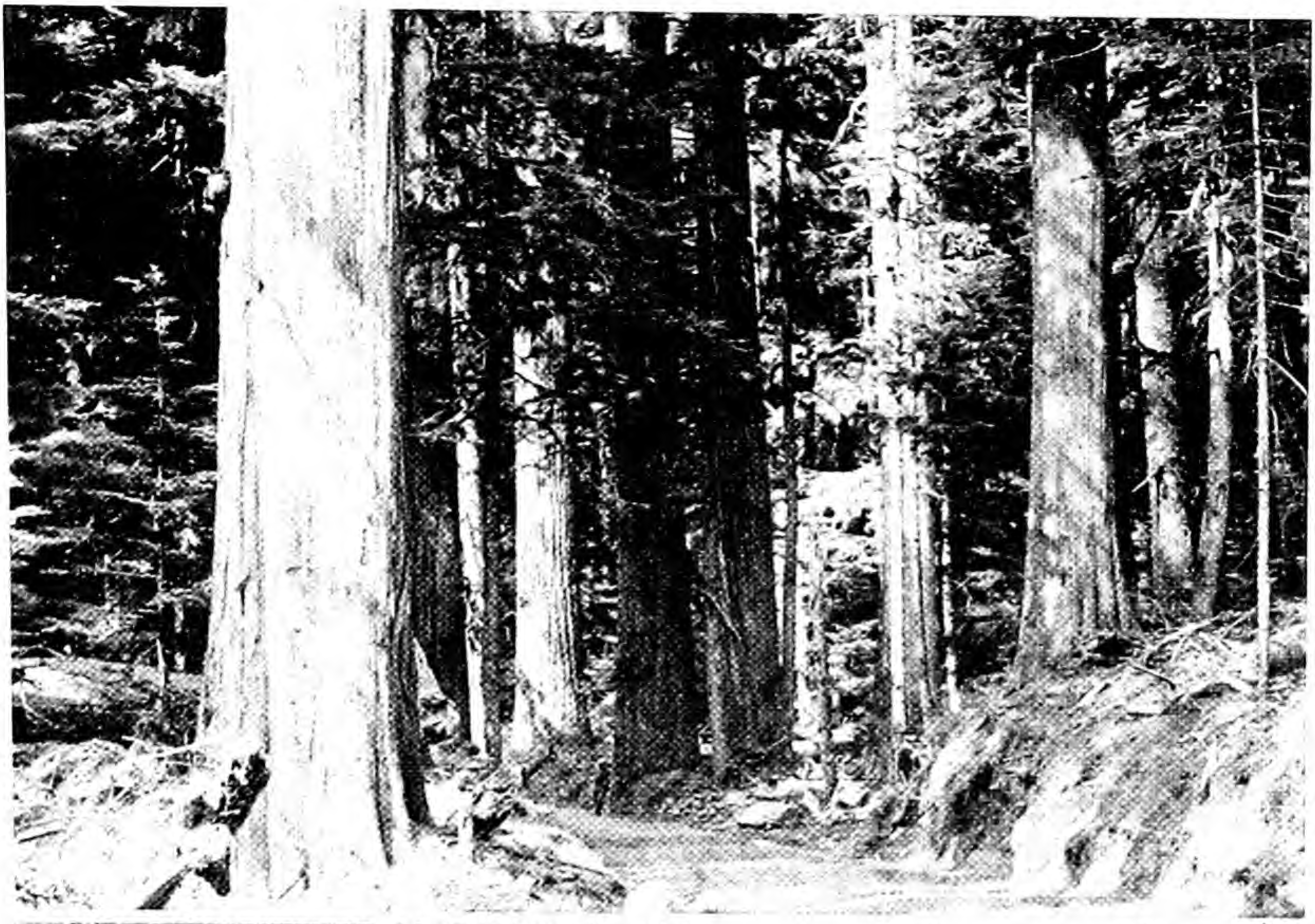
with it indications of habitat, structure and development which are not so obvious. Moreover, it involves important indications as to use, such as lumber, water regulation, grazing, etc. Indicators of former forests are either actual relicts of the forest itself or seral communities which mark particular stages of the successional reforestation. They may consist of the dominant trees as individuals or communities, of the subdominant shrubs or herbs of the climax forest, or of the dominants or subdominants of any successional stage. Their great value lies in the fact that they not only indicate the possibility of reforestation, but also the stage which has been reached and the further methods to be employed. They are by far the most important and practical of all forest indicators when the vast extent and significance of deforested areas are taken into account. They pass more or less gradually into indicators of the possibility of forest production in regions which have been repeatedly deforested and which show neither relicts nor seral stages of the original climax. Such are the transition regions between forest and scrub or prairie, in which the latter appear to be climax, but are really subclimax and will consequently yield to forest when artificial regeneration is employed. In addition, chaparral and grassland may also indicate afforestation in regions which have not borne forest for hundreds of thousands of years. These are primarily edaphic areas in which the indicator community owes its presence to a higher water-content resulting from soil or topography. Such are the sandhills of Nebraska and the river valleys throughout the prairie associations.

Kinds of Indicators.—Both the individual and the community may be used as indicators. The latter is naturally more complete and definite, but in many cases the change following clearing or fire is so complete that a single relict individual gives information of great value as to the original climax. This is true also of subclimax forests which have more or less completely disappeared in the reestablishment of the climax forest. The forest formation which is climax for a certain region is itself the indicator of the permanent type of the region, and hence of the forest which will naturally develop or redevelop in all cleared or bare areas. As a consequence, it is an indicator of site and likewise of the type of management to be used. Each association is an indicator of climate, while the various groupings and alternations of the consociations indicate different edaphic conditions as well. The societies indicate variations in water-content or light primarily, but the layer societies are especially

related to light. Differences in the density and growth of dominants and subdominants serve as indications of minor changes in the factor complex. Indicator values may be derived from growth in height, diameter or volume. The former is most convenient for use, but the latter is probably most accurate. Seedlings are among the best of dominant indicators, especially when their growth, habit and abundance are taken into account. The minute structure of leaves is an excellent indicator of light and water relations, and that of stems is an indicator of annual fluctuations in rainfall, and hence climatic cycles. Flowering and seed-production also have their indicator values, but these are of secondary importance.

Seral communities differ chiefly from climax ones in indicating edaphic conditions or habitats rather than climatic. Their peculiar advantage lies in the fact that they may at the same time indicate the nature of the initial area or disturbance, the particular stage of development in the succession and the habitat, and the final association or climax. Such stages are denoted by the associes, and minor stages or variations by the consocies, while the socies denotes subordinate differences within these. These three types of community, and the series of associes which constitute the sere, form a complete scale of variations and changes, upon which the problems of forest maintenance, or reforestation and afforestation, must be based. In short, while the climax indicates the permanent forest of a region, the seres indicate the methods and materials which must be used in hastening, maintaining, or postponing the climax community, which is inevitable under natural conditions. It is obvious that seral communities furnish indications from composition, density, and growth essentially similar to those of the climax.

Climatic Indicators.—It is axiomatic that all forest climaxes are indicators of forest climates (Plate 19). The four western formations, woodland, montane forest, Coast forest, and subalpine forest, indicate as many corresponding forest climates, while the scrub formations and especially the chaparral indicate climates in which water conservation is important. It is well understood that the three mountain climaxes indicate climates with a progressive increase of rainfall from woodland to alpine forest, while the Coast forest has the highest rainfall of all. In similar fashion, woodland, montane, and subalpine forest indicate a progressive decrease in the length of season and the temperature values, though the Coast forest marks the longest growing season and the most



A. Climax forest of *Pseudotsuga*, *Tsuga* and *Thuja*, Mount Rainier, Washington.
B. Climax subalpine forest of *Abies* and *Picea* as a climatic indicator, [illegible] Forest, California.

equable temperatures. The rainfall and temperature relations of the several formations have already been discussed in "Plant Indicators" (1920) and need not be repeated here. The associations indicate subdivisions or subclimaxes of the formational climates. In general, the Petran associations are drier and colder than the Sierran associations of the montane and subalpine climaxes. For the three woodland associations, the total rainfall varies less than its seasonal distribution, and the temperature relations seem more decisive than the rainfall. The pinyon-cedar indicates the coldest climate with much of the precipitation as snow, the oak-cedar the warmest, and the pine-oak the most equable. The first two have from 40 to 70 percent of their rainfall in the summer, and the latter about 20 percent. The two associations of the Coast forest show two subclimaxes strikingly different in both rainfall and temperature (Plate 20A).

The consociations serve to indicate still finer climatic divisions, both as to altitude and latitude, though in general their indications are merged in those of the association or formation to which they belong. This is well illustrated by the montane forest, in which *Pinus ponderosa* indicates drier and warmer climatic conditions than *Pseudosuga mucronata,* while *Abies concolor* is more or less intermediate. Consociations also indicate potential climates, with especial reference to the wet phase of the climatic cycle, where they form savanna, as in the case of *Pinus ponderosa* in the grassland climax, or *Juniperus* in the sagebrush. The varied groupings of consociations throughout an association also have some climatic indications, but these are often obscured by edaphic indications of more importance.

Edaphic Indicators.—These are either climax or seral dominants and subdominants. Seral dominants are typical edaphic indicators, since they mark the changing conditions of the habitat in its progressive development to the final climax condition. Climax dominants differ in their requirements and necessarily show indicator responses to local edaphic as well as general climatic conditions. Subdominants, whether seral or climax, mark minor differences in the habitat, and serve also to indicate the dominants in many cases where these have been destroyed or removed. The most striking edaphic indicators are the seres which arise in bare or denuded areas. Each prisere not only marks a particular type of initially bare area, such as water, rock, or dune-sand, but it also indicates the changes of the habitat complex, as well as the final climax. As already

mentioned, each seral stage or community denotes a certain set of factors, and at the same time the stages which are to come in the development of the climax. This is likewise true of subseres, which differ from priseres chiefly in arising in areas denuded by fire or other accident, or by the agency of man. They are much more numerous than priseres, the successional movement is much more rapid, and the stages fewer. Each subsere is an indicator of the disturbance process that originated it, and its stages mark the different degrees of development of community and habitat on the way to the climax. Such stages, or associes, occur in both subsere and prisere. Each marks a particular stage of the habitat which controls it, and in turn reacts upon the habitat to produce the next stage. It consists of two or more consocies, or seral dominants, which indicate minor changes in the stage and hence perhaps different areas of habitat. In addition, each seral community contains a varying number of subdominants which constitute socies, corresponding to the societies of climax communities. The socies mark the more minute differences of the habitat, and perhaps also the minor movements within the associes.

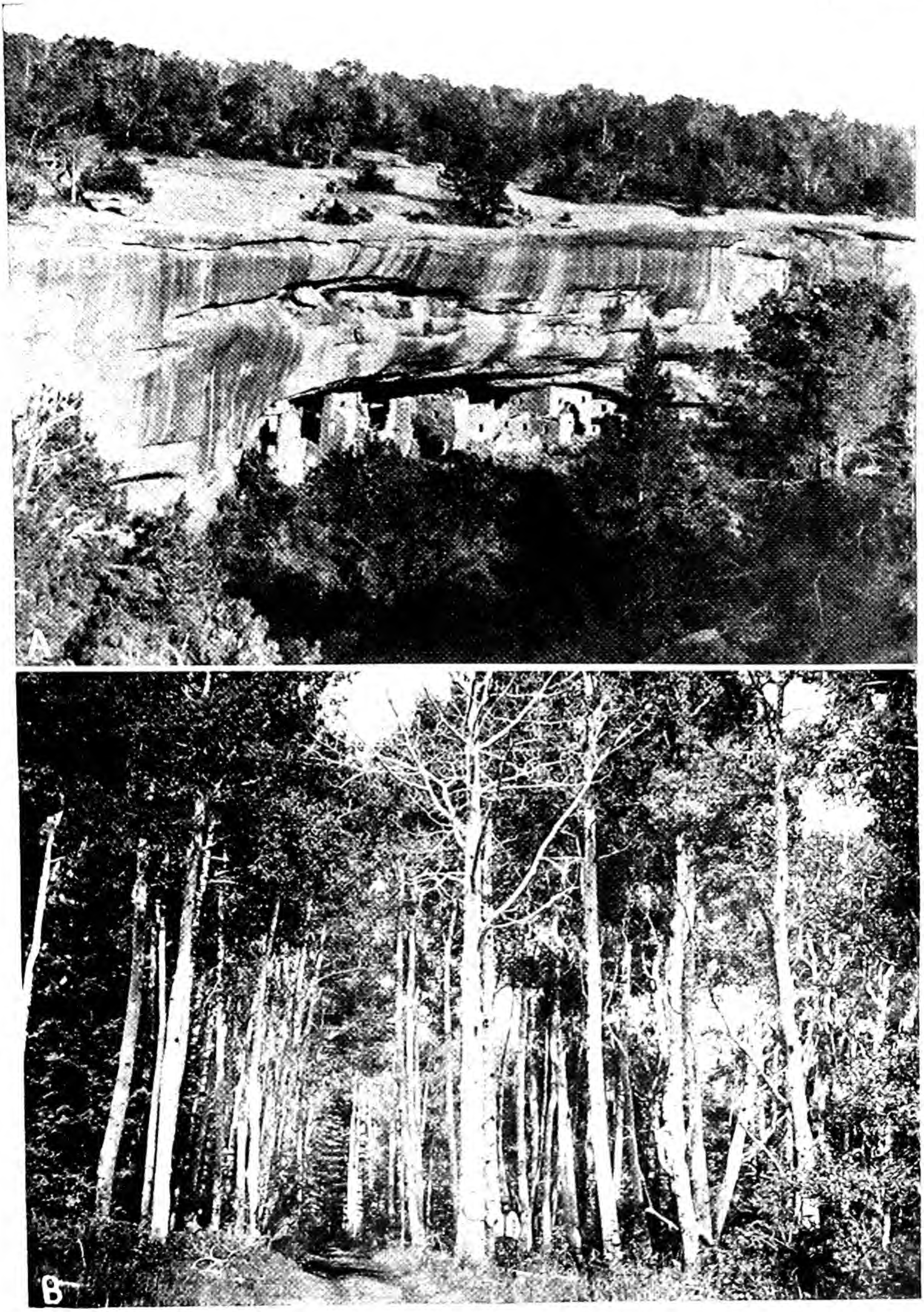
The most important edaphic indicators are those which denote differences in water-content, light, or soil, or mark the effect of disturbing agencies, such as fire, grazing, etc. In addition to the presence or composition of a community, its growth or the growth of one of its dominants serves as an indicator of variations in the habitat complex or of site quality.

Water-content Indicators.—In the several forest climaxes, the physical properties of the soil in relation to water-content are so much more important than the chemical that the latter require little attention. As a consequence, the indicators of water-content serve as indicators of soil texture, aeration, and temperature as well. The water relations of the climax and subclimax dominants have been considered briefly under each forest association. The climatic relations of the dominants of a community are reflected in the edaphic ones, and this may even be true of the dominants of different formations. The dominants of drier climates or subclimates take the dried slopes and ridges of the local area, and those of moister climates grow on northerly slopes and in canyons or valleys. *Picea engelmanni* frequently reaches the lower limit of the montane forest along the moist canyons of north slopes, while *Pinus ponderosa* extends to the middle of the subalpine forest zone or even higher on dry and warm south slopes. In short, dominants indicate the total

water relation, and hence their climatic indications may be completely subordinated to local conditions.

It is assumed that all dominants have different water requirements, and that each in consequence indicates a different water-content. It is believed that the results of further quantitative studies will show that the dominants of a sere can be arranged in a linear sequence from the pioneer stage to the climax. At the same time, it seems completely established that this sequence falls naturally into stages or associes, characterized by dominants of the same life-form and similar requirements. As a consequence, it becomes possible to use the dominants or consocies of a sere to indicate the successive small steps in the changing water-content from the initial, bare or denuded area to the climax, while the associes indicate the stages of longer duration which are characterized by a certain set of water conditions. In the prisere, such conditions and their indicators have some relative permanence, but in the subsere the successional movement is much more rapid and the stages sometimes obscured. In both cases, however, the basic principle holds that a complete series of indicators marks the changes of water-content from an originally hydrophytic or xerophytic bare area to the relatively mesophytic forest climax. The exact value of each community or dominant as an indicator must await more general quantitative study, but the approximate values that can be assigned them at present are of genuine service to forest problems.

Light Indicators.—In spite of the fact that small differences in light values are more readily detected by observation than is the case with water-content, the recognition and use of plants as indicators of different light intensities are matters of recent development. The forester has long understood the general importance of light in the forest, and his tables of tolerance are an indirect recognition of indicator values. As long as he was chiefly interested in silviculture, however, tolerance was a matter of relative growth in the same or similar situations. The development of silvics as a phase of ecology directed attention more to the factors of the habitat, and led to the use of photometers for measuring light intensity. This has made possible the correlation of tables of tolerance with measured intensities and the use of the dominants concerned as direct indicators. Such work has merely been begun, however, and much quantitative study will be required before the general values of tables of tolerance can be made exact. Measurements of light intensity have been largely confined to forests, but it is clear that light values have considerable im-



A. Pinyon-Cedar association indicating a cold climate, Mesa Verde, Colorado
B. Competition for light: *Picea engelmanni* somewhat suppressed by *Populus tremuloides*, Uncompaghre Plateau, Colorado

portance in other communities as well. This is especially true in woodland, scrub, and savanna, but it holds also for grassland, particularly the tall grass prairies (Plate 20B).

Two facts must be taken into account in correlating light indicators with measures of light intensity. One of these is the effect of variations in the composition or quality of the light. There can be no question that white light is modified in passing through the leaves of the forest canopy, the red and blue being absorbed to a larger degree than the green and yellow. In the case of conifers practically no light passes through the needles, and the light beneath them is white light, which has passed through the openings between the needles. In the case of broad-leaved forests, the amount of light entering between the leaves decreases with increasing density of the canopy, and that modified by transition through the leaves becomes correspondingly more important. In all forests studied by the writer, the light has been essentially normal in composition, and reduction in intensity seems to have much greater influence than any change in quality. Forests of *Picea engelmanni,* in which the light is practically normal, suppress the undergrowth even more completely than those with actual differences in quality.

The significance of light indicators is also complicated by the influence of other factors. Although this is the rule for all factors, it is more marked in the case of light than of water. This is partly because light affects fewer functions directly, and partly because the modifying influence of water upon tolerance has been too much ignored. It is perfectly clear that the intimate interaction of water and light in competition, especially in forests, makes it necessary to take them both into account in determining tolerance as well as indicator values. This is true to a much smaller extent of nutrients and temperature, but these would have some influence wherever they tend to become limiting factors. Furthermore there can be little question that light is usually the controlling factor in tolerance wherever the canopy is closed and that water plays a decisive part only when the light intensity is higher and evaporation and competition consequently greater.

Forest dominants are among the simplest and most direct of all light indicators, since they constitute actual experiments in planting, natural or otherwise. As indicators they have the same unique value as crop plants and, so far as practice is concerned, make the use of less direct indicators and of instruments more or less superfluous. In many cases, however,

seedlings of a particular dominant or of all the related ones are absent from the forest floor, or the forest itself may be represented only by the undergrowth or certain elements of it. In such cases, the subdominant shrubs and herbs must be used as indicators. The latter in particular are often more sensitive than the trees themselves and hence furnish a more exact scale of indications. The widespread occurrence of certain herbaceous societies throughout one or more forest associations, or even formations, affords a striking opportunity for correlating the light relations for dominants associated under varying conditions as to other factors. The perennial herbs are of especial importance in this connection, as the effects of differing light intensities are clearly reflected in a variety of ways, in density, form, height, flowering, etc.

In definitizing the use of light indicators, it will be necessary to resort more and more to quantitative measurements of responses and factors. The most important responses in this connection are photosynthesis and growth. Both of these have certain values, and they will be more and more used in combination, as complete and accurate results become necessary. At present, however, the determination of photosynthesis and its correlation with light is a much simpler and more exact process. As a consequence, the best determination of indicator values for light will continue to be initiated by close observation of general correspondences, which are first tested by means of measurements of intensity, and then by studies of photosynthate production. It is probable, indeed, that this will give the real light indication without recourse to growth responses, but the latter will prove necessary to obtain the full indicator value for practical purposes.

Site Indicators.—The term site like forest type, has a wide range of meaning among foresters. While it is regularly used to denote the habitat, it is applied to all possible divisions of the latter. This is understandable, since this is the present ecological practice in the case of habitat. But just as it has proved necessary to distinguish habitats of different character and various degree, so it is desirable to recognize several categories of site. Climax and seral habitats or sites are fundamentally different, though they are often found side by side. The habitat of one consociation differs from that of another of the same association, and mixed areas of the two show subordinate differences. Finally, the same consociation exhibits marked variations in growth and density, each corresponding to smaller differences of the factor-complex.

In practice, the forester has emphasized two of the several categories of sites. The first is the consociation habitat or the site occupied by a dominant, and the second the minor sites marked by significant differences in the growth or density of a particular dominant. As a matter of fact, the two types are developmentally connected, the growth sites, commonly designated as I, II, III, and IV, representing a sequence of minor habitats within that of the dominant consociation, such as *Pinus ponderosa, Pseudotsuga*, etc. The recognition of growth sites is chiefly important in connection with yield tables and working plans. In planting operations, consociation sites must first be determined, and then growth sites may be used to ascertain the most promising areas.

Growth as an Indicator.—As already discussed, the presence of a dominant furnishes one set of indications, and its growth, another. The latter naturally affords a more sensitive scale of measurement, and hence indicates the effective differences of the habitat in terms of timber production. It is obvious that total growth is the most complete indicator, though it is equally clear that height-growth or even width-growth may be used with much success. Since readiness and convenience are essential to the practical use of indicators, height-growth has received the most attention at the hands of those interested in the classification of sites.

It is highly probable that water-content is the factor that exerts the primary control upon height-growth, and width-growth also. However, it seems practically certain that the competition for water and food between the growing points and the cambium ring determines that height-growth shall largely precede width-growth during each year as well as during the life-history of the individual. The studies of Brewster (1918) indicate that "the height-growth of larch seedlings does vary in accordance with variations in weather conditions from year to year, and that the most favorable conditions for rapid height-growth are produced in the North Idaho region by a combination of temperatures somewhat above the average, coupled with a high percentage of clear days, with an average amount of precipitation evenly distributed in the form of good rains at intervals of four to ten days preceded and followed by lighter showers." The greater rainfall, lower temperature, and greater cloudiness of northern Idaho in comparison with northern Arizona readily explain the relatively greater importance of temperature and light in height-growth, as well as the difference in the seasonal occurrence. This must be expected

for the various climax formations, for which the task of correlation is primarily one of discovering the limiting factor by the measurement of the habitat complex.

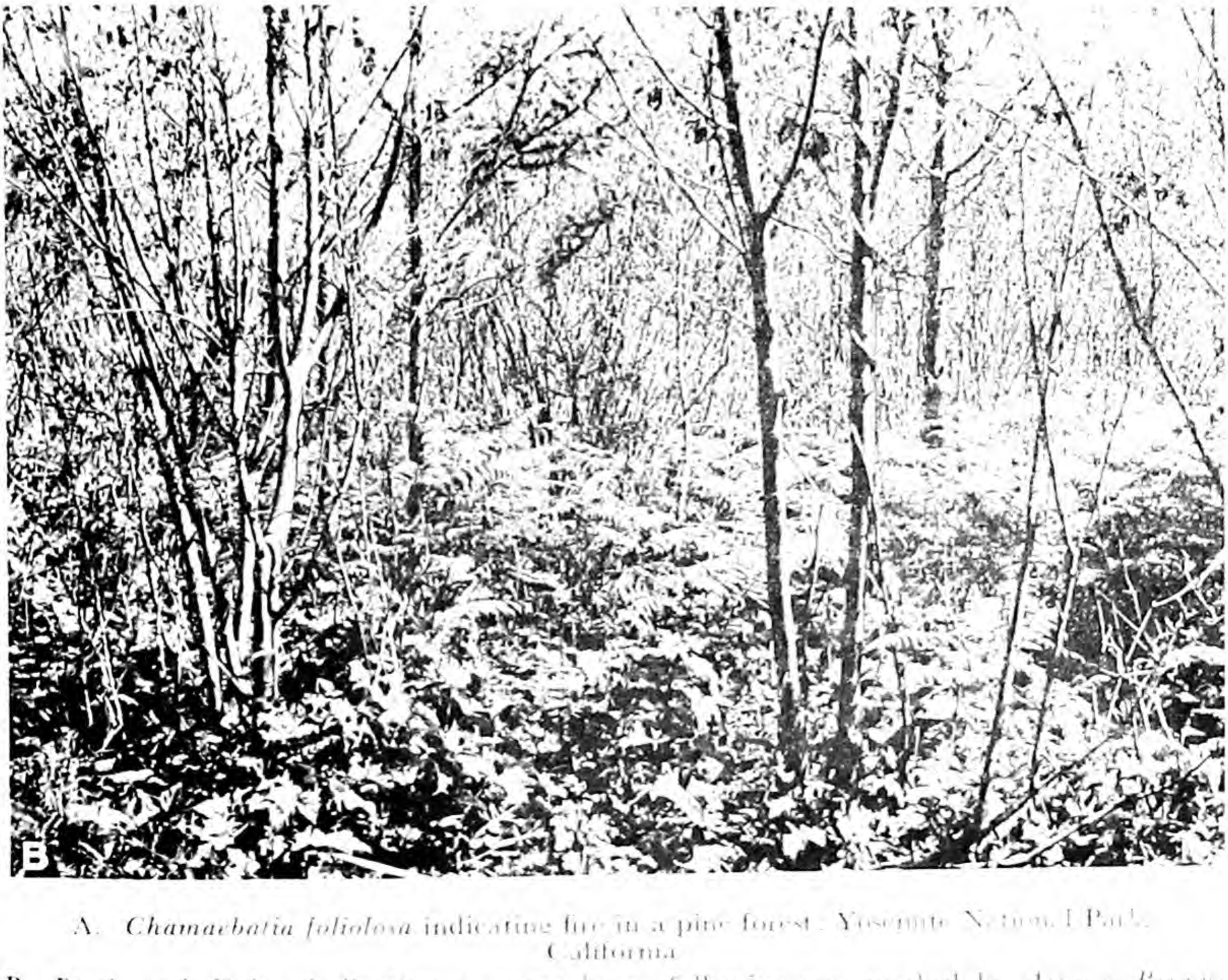
In the determination and classification of sites, as well as in their discussion, it will conduce to clearness to recognize that this is almost wholly a matter of applying the indicator method. While the word site appears to refer to the physical conditions, it does so only in so far as these are indicated by the presence or growth of the species concerned. And while it is felt that the species affords a better measure than instruments do, such a measure is one of actual growth and not one of the controlling or limiting factors. Hence it must be recognized that height-growth indicates habitat only in a general way, and that its specific indications apply only to the productiveness of the area in terms of a particular tree crop.

Burn Indicators.—It is a general rule that subclimax dominants serve as the typical indicators of forest burns. This is in conformity with the principle that almost any consocies and many socies of the subsere may indicate fire as well as other similar disturbances, the particular initial stage depending upon the degree of disturbance or the frequency of its repetition. The universal occurrence of tree and shrub consocies as burn indicators is explained by the fact that fire not only produces areas temporarily free from the competition of the climax species, but also characterized by conditions favorable to less exacting species. Their characteristic dominance is chiefly due to the rapidity and completeness with which they occupy the ground, as a consequence of excessive seed production, the opening of cones by fire, or the ability to produce root-sprouts. The conifers rely almost wholly upon the first two methods and chiefly the second, while the deciduous trees depend mainly upon root-sprouts. Among trees, the three types are represented respectively by *Pseudotsuga* and *Larix*, such pines as *Pinus contorta* and *attenuata*, and by aspen, birch and alder. The scrub indicators owe their character almost wholly to root-sprouting, reinforced more or less by seed production and mobility.

The burn subsere consists of the usual stages of annual and perennial forbs, grasses, shrubs and trees. However, the number and distinctness of the stages and the duration of the subsere depend chiefly upon the severity of the burn. In the most severe burns the initial community often consists largely or wholly of mosses and liverworts (*Bryum*, *Funaria*

and *Marchantia*), and is followed by one of annuals, and this by one of perennials. The species, and to a less extent the genera, of these vary with the climax association, but such species as *Agrostis hiemalis, Epilobium spicatum, Achilleia millefolium,* and *Pteris aquilina* are more or less universal. The development of a grass stage is less regular, since its place is often taken by scrub when the root-sprouting shrubs are abundant. The scrub is normally replaced by aspen, birch or alder, and these may yield to a subclimax forest, such as that of lodgepole pine, or be replaced directly by the climax. It is obvious that fire may sweep through the scrub, aspen or lodgepole communities, and initiate new subseres, producing an intricate pattern of seres and communities. In the great majority of cases, the succession is more or less telescoped, and often completely so. The root-sprouting ability of the shrubs and aspen and the release of seeds enclosed in cones or buried in the duff enable the shrubs and trees to begin development the first year, at the same time that the herbs appear. In such cases, practically all the dominants appear at once, but the development still exhibits many of the features of succession. The stages, though brief, give character to the area in the normal sequence and each disappears in turn as the competition of the next one becomes too great for it.

For the reasons just given, the herbs are relatively unimportant indicators in complete burns, though they are characteristic in the case of light ground fires. The burn subsere is characterized almost wholly by scrub, deciduous woodland, or subclimax forest, not only because of the duration of the latter, but also because repeated fires tend to make them relatively permanent. On account of differences of distribution as well as the general similarity in requirements, the three types rarely occur in the same subsere. Two, however, are frequent, aspen and lodgepole being the most common. This is in accord with the occurrence of lodgepole as the characteristic burn community in the northern Rocky Mountains, aspen in the southern, and scrub in the Southwest and in California. As burn indicators, they have several features in common, in spite of their differences in life-form. They not only indicate the possibility of reestablishing the climax by preventing fire in some cases or by planting in others where the original climax dominants have disappeared, but they also make it clear that artificial means and fire especially must be resorted to in areas where it is desirable to maintain the subclimax as a relatively permanent type (Plate 21).



A. *Chamaebatia foliolosa* indicating fire in a pine forest, Yosemite National Park, California.

B. *Pteris* and *Rubus* indicating a recent burn, following one marked by [illegible] associes, *Pseudotsuga* forest, Eugene, Oregon.

The importance of burn climaxes has been emphasized by Clements (1910) in the case of the lodgepole pine, as follows:

"The lodgepole forest is the key to the silvicultural treatment of the forests of the eastern Rocky Mountains, especially in Colorado and Wyoming. Its position in a zone between Douglas fir and yellow pine below, and Engelmann spruce and alpine fir above, gives the forester a peculiar advantage. Its enormous seed-production, the power of the seeds to remain viable in the cones for years, its preference for soils of moderate water-content, the dependence of reproduction upon sunlight, and its rapid growth are all points of the greatest value in enabling the forester to accomplish his results. And it is by means of fire properly developed into a silvicultural method that the forester will be able to extend or restrict lodgepole reproduction and lodgepole forests at will."

The relation of aspen to lodgepole in burn subseres and its role as a temporary type have been dealt with in the same study. The significance of aspen as a burn subclimax and its importance as a temporary type have been discussed by Pearson (1914), Sampson (1916), and Baker (1918), while Hofmann (1917) has made a study of extensive burns in the Northwest where *Pseudotsuga* forms a remarkable subclimax.

Scrub communities are regular indicators of fire where they are in contact with forest. In fact, sagebrush appears to be a fire subclimax in the pinyon-cedar woodland, as well as in the southern portion of the Coastal chaparral. Chaparral, however, is the typical scrub indicator of fire in woodland and forest. This is as true of the subclimax chaparral along the eastern edge of the grassland climax as it is of the Petran and Coastal associations. The most characteristic development of chaparral as a burn indicator is found in the montane forests of California, where the scrub persists as a more or less complete forest layer. Chaparral owes its importance as a fire indicator to its remarkable ability to form root-sprouts, and hence the form of the dominant shrubs is itself a response to fire. Fire in chaparral leads to a short subsere, in which the herbaceous stages persist for only a few years before the new shoots overtop them. Repeated fires may produce a subclimax characterized by *Eriodictyon,* or by *Artemisia, Salvia,* and *Eriogonum.* In the region of its contact with woodland and forest, chaparral is an indicator of forest burns, and consequently is subclimax. This is true in both associations, but is more marked in the Sierran, perhaps because of its greater massiveness, Munns (1919) has assumed that all of the latter is a temporary type due to fire,

but this certainly seems not to be true of the regions with 12 inches or less of rainfall. This assumption is largely due to a misconception of what constitutes the test of a climax. Both of the tests used, the successful planting of trees and the existence of scattered trees and tree stands, would prove the grassland climax to be a temporary one. The typical processes in the establishment of a forest are seed-production, dissemination and ecesis, and artificial planting is powerless to throw light upon the outcome of these. Further studies of the chaparral formation during the past three years have confirmed the view expressed in 1916 that it constitutes a real climax, though portions of it are undoubtedly subclimax. This view is supported by the conclusions of Cooper (1922), who has made an intensive study of the California chaparral upon the instrumental and successional basis.

Grazing Indicators.—With reference to the forest itself, only those grazing indicators are of importance that indicate overgrazing, and hence actual or potential damage to the reproduction. The presence of the usual overgrazing indicators would serve this purpose, but these are usually accompanied by evidences of damage to the seedling as well. However, while abundant evidence of this nature denotes overgrazing, it is still a question as to just when this becomes critical in the reproduction of the forest. In fact, it is clear that the critical degree of overgrazing depends much upon the nature of the community, time of year, age of the seedlings, and other factors. Much light has been thrown upon the problem by three careful studies in the national forests. Hill (1917) has studied the damage to seedlings in the yellow-pine forests of northern Arizona, Sparhawk (1918) has shown that the damage to seedlings more than a year old is negligible in the yellow-pine forests of central Idaho, and that the mortality of seedlings less than a year old averages 20 per cent, and Sampson (1919) studied the effects of grazing upon aspen reproduction (Plate 22).

Cycle Indicators.—Trees, and shrubs also, may serve as indicators of climatic cycles by virtue of their growth, seed-production or reproduction. In addition, there appears to be a certain correlation between the frequence and intensity of forest fires and the dry and wet phases of the cycle. The growth of trees as recorded in the annual rings is the classic material for the studies of Douglass, Huntington and Kapteyn upon climatic cycles. The width of the ring indicates the varying rainfall of different years so clearly that Douglass (1919) has found it possible

A. Pine reproduction in an exclosure: Fort Valley Experiment Station, Flagstaff, Arizona.
B. Reproduction cycles of *Picea engelmanni;* Uncompaghre Plateau, Colorado.

to cross-identify rings from trees grown many hundreds of miles apart. He has also found that the yellow pines of central Arizona often indicate two growing periods in one year by the formation of a double ring, and Shreve (1917) states that this appears to be regularly the case with trees at 6,000 feet in the Santa Catalina Mountains. It seems almost certain that height-growth and volume will likewise show cycle correlations, and this is suggested by Pearson's results in the study of the relation of height-growth to spring precipitation in northern Arizona. The suggestion that seed-production is related to climatic cycles is based upon its well-known periodicity, as well as upon the fundamental fact that as a growth response it is controlled primarily by water and temperature. It seems probable that the seed-production cycle of pines especially is a response to the interaction of the 11-year cycle and the excess-deficit cycle of 2 to 3 years.

Reproduction reflects more or less faithfully the variations in rainfall during the 2 to 3 year, the 11-year, and the 22-year cycles. This correlation is clearly seen in the case of woodland and montane forest, especially at the lower limit, but it is naturally less evident in climaxes with a higher rainfall. It is most striking where woodland or forest is in contact with a community of lower water requirements, such as grassland, sagebrush, or chaparral, and shows less in the reproduction on the forest floor. All the cases of tree savanna and "natural parks" so far investigated warrant the working hypothesis that reproduction in such areas is cyclic and corresponds as a rule to the 11-year cycle, though minor variations conform to the 2 to 3 year cycle. There is also considerable evidence that the success or failure of planting operations has often been determined by their accidental coincidence with the wet or dry phases of the 11-year cycle, while it is obvious that in the future, planting should be carried out with reference to the phases of the 2 to 3 year and 11-year cycles.

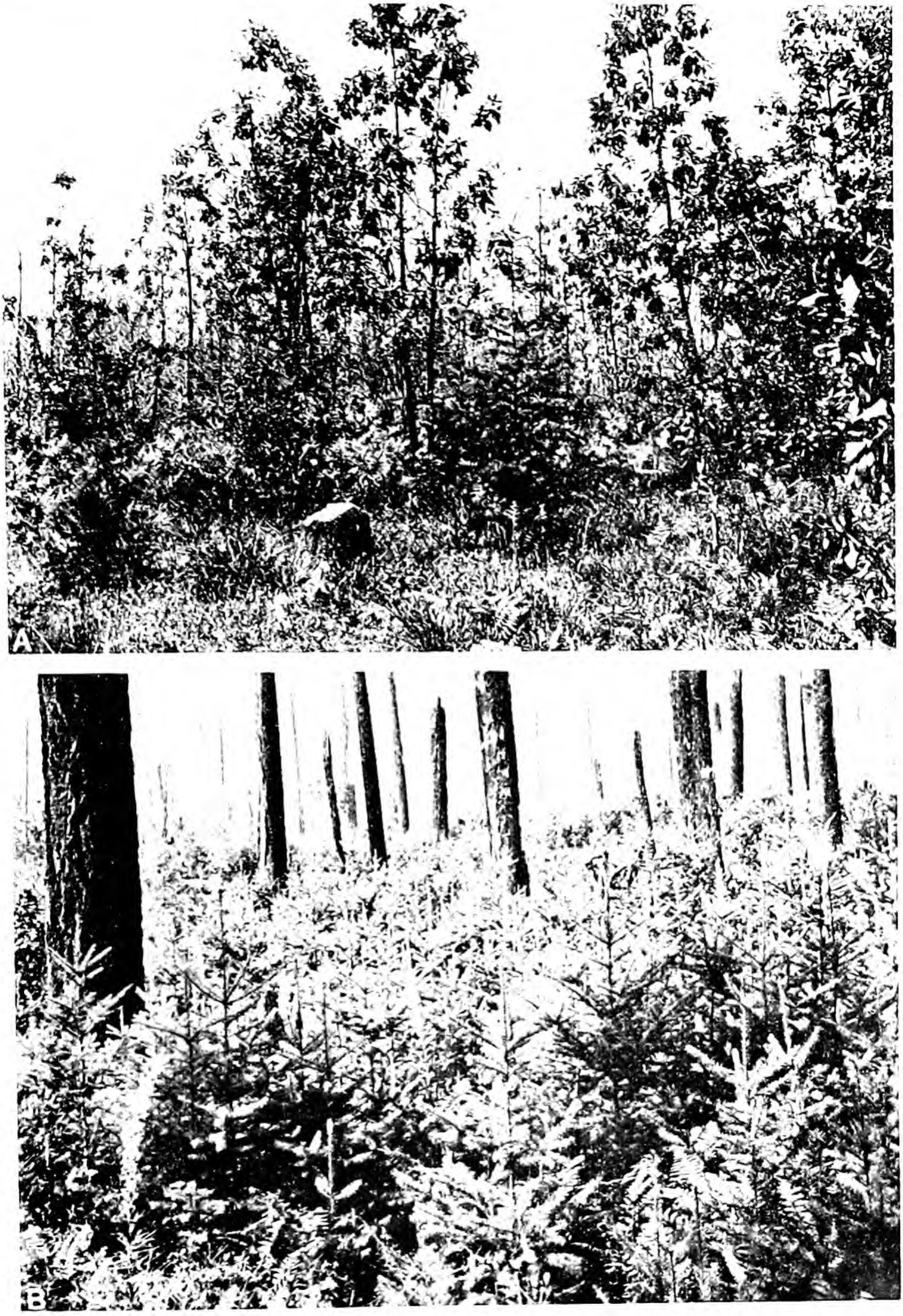
Planting Indicators

Kinds.—Indicators of sites for planting are of two kinds: (1) those that indicate the former presence of forest; (2) those that suggest the possibility of developing forest in grassland or scrub areas. The first are indicators of reforestation, the second of afforestation. The obvious indicators of reforestation are relict survivors, or trunks and stumps. Less obvious but equally conclusive are charred fragments or pieces of charcoal in the soil. In those cases where there is no direct evidence of the

original forest, the desired clues are readily afforded by indicator communities which bear a definite relation to the forest. Such are seral and especially subclimax communities which exhibit a successional relation to the forest climax, and such societies of shrubs or herbs which formed layers in it. While the latter are frequent in burns and clearings, they are usually accompanied by tree relicts which furnish more direct evidence. In some cases, however, they are the sole indicators of the former existence of forest in a particular spot. Subclimaxes are by all odds the best indicator communities of forest climaxes, since they show that the habitat has reached the condition in which the climax dominants can thrive. The earlier communities of a subsere have nearly the same value, since the habitat undergoes relatively slight change. In the case of a prisere only the grass and scrub stages indicate that the slow reaction upon the originally bare area has reached a point in which remaining changes may be compensated by planting operations. Afforestation indicators are savanna, chaparral, or grassland of tall grasses, in which the water requirements are sufficiently near those of trees that the gap may be bridged by planting methods, and especially by making use of the increased rainfall of the wet phase of the climatic cycle.

Furthermore, the indicators of sites for planting or sowing serve also to indicate the preferred species. In the case of reforestation, the general rule is that these are the climax trees that were in possession, but reasons of management may make it desirable to use a subclimax dominant, such as lodgepole pine. Similarly, the growth-form best adapted for planting in a region is the one developed by that region, as the Forest Service has repeatedly demonstrated at its experiment stations. In the case of afforestation, the indications as to species must be derived from tree communities somewhere in contact with the grassland or scrub, as from pine in the case of the sandhills of Nebraska, from the indications of an intermediate community, such as scrub, or from the comparative study of habitats.

Prerequisites for Planting and Sowing.—The critical part played by rodents and by competition in natural reproduction was recognized some forty years ago (1910), and extentive tests of sowing in many national forests by the Forest Service has shown that destruction or control of the rodents is imperative. In fact, it seems evident that for practically all regions rodents are the most serious enemies of both natural and artificial reproduction, and that they should be systematically and permanently



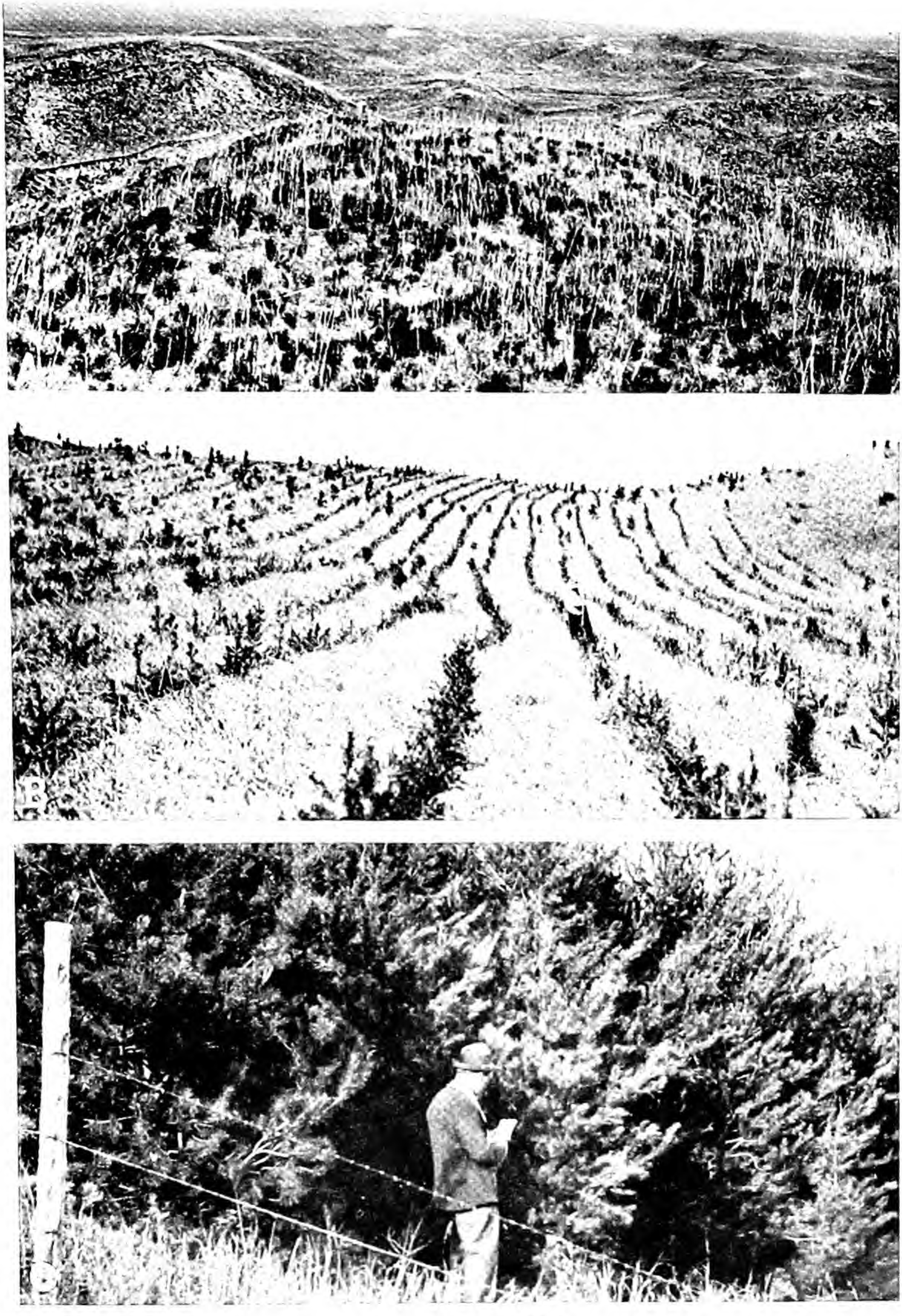
A. *Arbutus* as an indicator for reforestation, *Pseudotsuga* forest; Eugene, Oregon.
B. Burn reproduction of *Pseudotsuga* from seed in soil; Wind River Experiment Station, Washington.

cleared out of all areas in which reproduction is important. Competition is a process which is less readily controlled on a larger scale. Competition for water is much more decisive as a rule than for light, the latter usually becoming critical only in dense scrub or similar communities. The disturbance of the soil involved in planting seedlings or in sowing by the seed-spot method usually suffices to reduce water competition sufficiently, except in a grass sod. This is most frequently encountered in clearings and in grassland associations in which afforestation is the method to be used. In climax grassland, where the annual rainfall is less than 25 inches, the grasses use all of the water-content during the drier portions of the season. As a consequence, seedlings or transplants have little chance of survival unless the sod is destroyed about them, or unless planting is done during a period of unusual rainfall. As a desirable precaution under all conditions, the competition of the grass cover should be decreased by such treatment as the density of the sod and the nature of the soil will permit.

Reforestation and Afforestation Indicators.—The indicators of the possibility of forest production in grassland and scrub climaxes are either such extra-regional communities of trees as are found in savanna or in the fringing woods of river valleys, or such grasses and shrubs as indicate an approach to the water requirements of trees. As a matter of fact, practical afforestation has been confined chiefly to the sandhill regions of Nebraska and Kansas, in the first of which all four of these indicators have been present in some degree. Indeed, the success of planting in Nebraska and its failure in Kansas are related to the fact that these indicators were present in the one State and largely lacking in the other. While it is clear that no sharp line can be drawn between reforestation and afforestation, the latter is regarded as having to do only with those climaxes, grassland and scrub, in which trees occur at the margins or in valleys. While pine savanna and valley woodland were doubtless more extensive in the sandhills of Nebraska during the wet phase of some of the major climatic cycles of the present geological period, it is practically certain that this region has belonged to the grassland formation since the Miocene at least (Plates 23 and 24).

3. Grazing Indicators

Kinds of Grazing Indicators.—The simplest and most obvious indication of a plant community is that which denotes the possibility of graz-



Forestation in the sandhills of Halsey, Nebraska

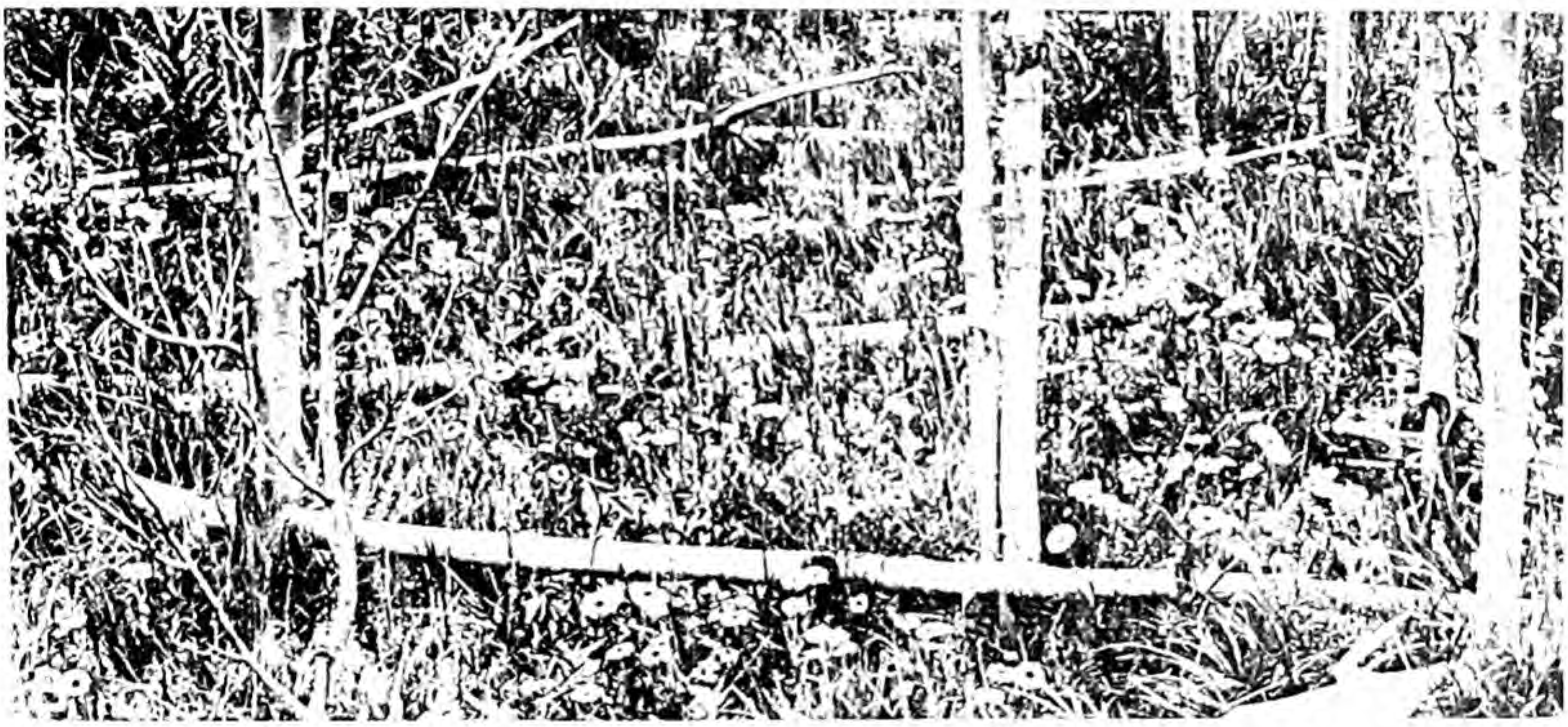
A. *Andropogon-Calamovilfa* tall grass postclimax, indicating high chresard and the possibility of afforestation

B. Three-year-old plantation of jack pines (*Pinus divaricata*)

C. Jack pines 10 years after transplanting

ing. Today this is so axiomatic for grassland and scrub associations as to be entirely taken for granted. This has not always been the case, however, and even at present there are forest and seral communities in which grazing indicators furnish a decisive test of the desirability of utilizing them. In the first instance, grazing types may be grouped as grass, weed, browse, and forest, and used to indicate the kind of grazing. The general principle in effect here is that a uniform community of grass, weed, or browse indicates cattle, sheep, or goats, respectively, while a prairie or a grass-scrub mixture or savanna denotes mixed grazing of two or three kinds of animals. The most striking and useful indicators are those which have to do with grazing capacity and overgrazing. These make it not only possible to measure the amount of grazing capacity and the degree of overgrazing, but they also reveal any failure to secure proper utilization. In addition, they serve to indicate the annual variation in forage production and to permit the correlation of these with the wet and dry phases of the climatic cycle. They likewise disclose the effect of local disturbances, especially those due to rodents, and they furnish a means of tracing the effects of eradication. As a consequence, they afford a complete basis for maintaining a proper balance between the utilization and conservation of the range and are of the greatest service in developing and applying an adequate system of range or ranch management.

The grouping of indicator communities as grass, weed, browse, and forest is one of both general and practical value. It permits subdivision into as many minor communities as desirable, and the chief consideration is to correlate these as naturally and effectively as possible. For this, no system approaches in value that of the developmental relationship as exhibited in the various climaxes and their successional stages. The climaxes indicated later illustrate the three main types, grass, scrub, and forest, while the seral communities and subdominants frequently exemplify the weed type as well. With reference to the grazing value, however, forest and woodland are to be classified on the basis of their undergrowth as grass, weed, or browse. It makes little difference practically whether grazing types are first grouped on the basis of their nature as grass, browse, etc., or on that of development, as climax and seral. The best system will necessarily employ both, but the vast extent of the climaxes and their obvious dependence upon the vegetative form suggests them as the preferred basis. This has the further advantage of making the practical and the ecological system the same and of avoiding the



A. Grass type, *Andropogon-Buchloe-Bouteloua*, Smoky Hill River, Hays, Kansas.
B. Weed type, *Erigeron*, *Geranium*, etc., in aspen forest, Pike's Peak, Colorado.
C. Browse type, *Artemisia tridentata*, Beulah, Oregon.

confusion which exists in forestry, where the practical types and ecological units are often wholly different. The developmental method is also desirable in that it furnishes a uniform method of dealing with finer and finer divisions upon the basis of climate, soil, and region, as well as upon that of ecology and floristic. As all of these enter into practice sooner or later, it seems clear that the best treatment of grazing indicators is that which relates them to the proper formation and association. In consequence, the following discussion deals first with climax communities as indicators as much the most important, and then with the more localized seral communities. In addition, some account is taken of artificial communities due to planting or other modification, since it is assumed that these will play an increasingly larger part in the grazing industry of the future (Plate 25).

Significance of Climax Types.—The value of the climax community as an indicator rests primarily upon the characteristic life-form. This is clearly seen in the three types, grass, weeds, and browse, but in the case of forest it depends upon the life-forms of the layers and seral stages. Climax formations are far more extensive than the developmental stages which occur here and there in them. Moreover, such stages are constantly moving toward the climax condition, slowly in the case of priseres and rapidly in the case of subseres. The climax communities are extensive and permanent, the seral ones local and temporary as a rule. As a consequence, the grazing practice of large regions must be based upon the indications of the climax formation or its subdivisions, while in a particular locality the importance of certain seral communities may demand some modification in practice. Apart from the vegetation-form as shown in grass, forb, shrub or tree, the habitat-form and growth-form of the dominants must also be taken into account. Communities of sod-forming grasses indicate different values and treatment than those of bunch grasses, while there is a striking difference between the associations of tall grasses and of short grasses. Climax communities of dominant forbs do not exist, but prairies and alpine meadow often contain so many mixed societies that the grazing value depends largely upon them.

Formations as Indicators.—As has just been seen, the grazing value of a climax is determined primarily by the vegetation-form, though other factors enter locally to modify it more or less. The grassland climax is by far the most important of all, and there is little doubt that its development and extension have controlled the evolution of grazing animals in

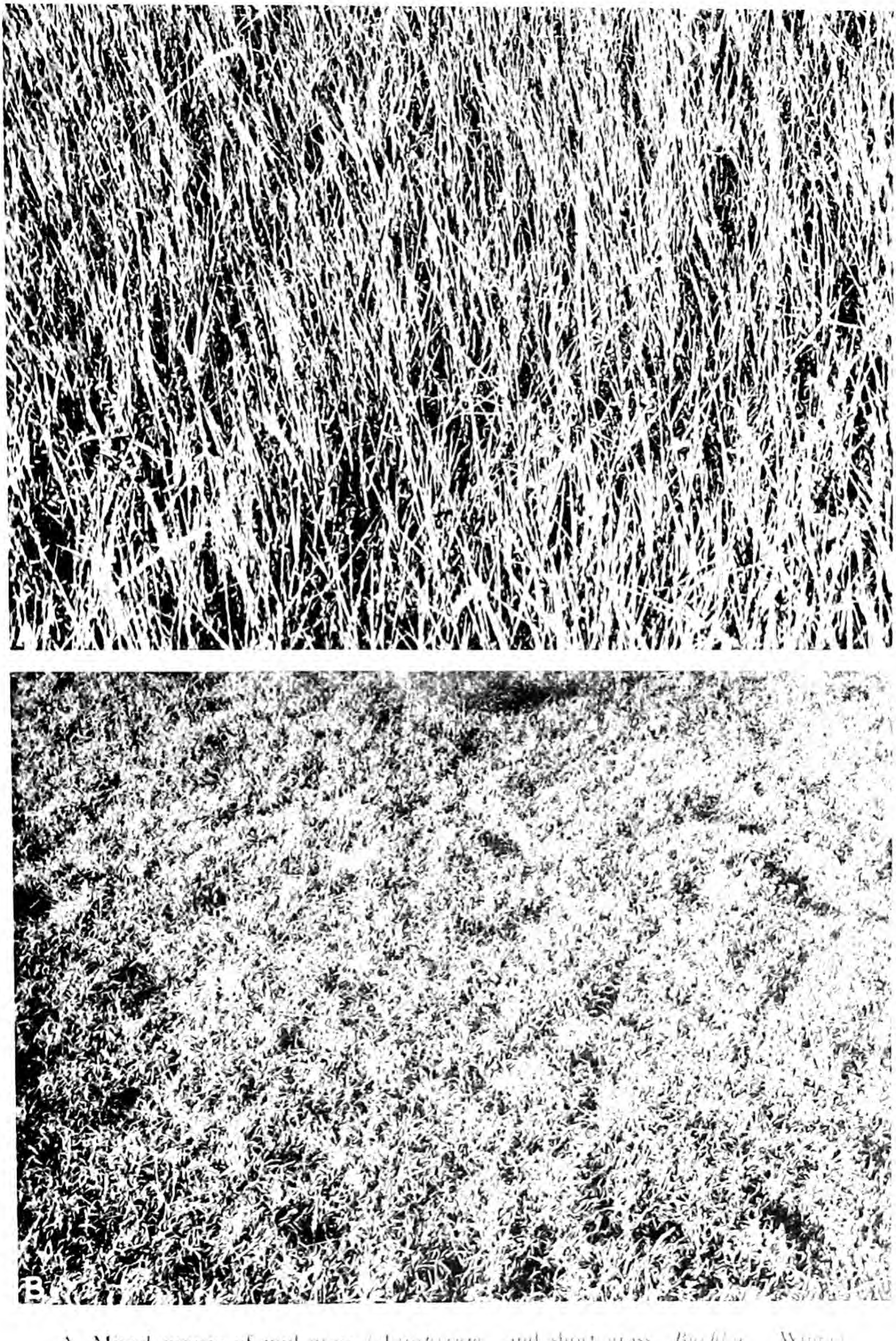
the past. The fact that the word *graze* is formed directly from *grass* proves that grassland has long been the primary grazing type, and that all others are secondary, resulting from the natural extension of grazing into scrub and forest. The alpine meadow ranks next to prairie and plain in primary grazing value, though the short season finds expression in the low growth-form as well as in the short period for grazing. The savanna marks the transition from primary grazing land, *i.e.*, grassland to scrub. In spite of the unique importance of the latter for mixed grazing, its actual grazing value is secondary, as is indicated by the word *browse* applied to it. Of the scrub climaxes, the chaparral usually stands first in importance, the sagebrush next, and the desert scrub last, though this varies greatly with the grouping of the various dominants. Of the forest formations, montane forest has the greater value, due largely to the open grassy nature of the yellow pine consociation. The woodland resembles the latter more or less and often ranks next to it in amount of grazing. The subalpine forest varies greatly in importance. The grazing value of its meadows, natural parks, and aspen areas is high, but the climax forest is uslly too dense and closed to permit the growth of a uniform ground cover. This is even truer of the luxuriant Coast forest, in spite of the fact that it often exhibits a dense tangle of shrubbery.

Associations as Indicators.—The indicator significance of an association is essentially that of the formation to which it belongs. As a subdivision, it represents a closer response to regional conditions, and the various associations of a climax permit the recognition of more or less different grazing values. This is characteristically true of the grassland and alpine meadow formations. It holds to a somewhat smaller degree for the scrub and is least evident for the forest climaxes, in which the number and extent of seral communities are more significant for grazing than the climax areas themselves.

In determining the relative grazing value of the associations of the grassland climax, this is found to depend upon density, height and mixture. Upon this basis, the subclimax prairies are perhaps the most valuable, though the true prairies are nearly equal, and in some cases even superior. The mixed prairies come next. The bunch grass prairies at their best may equal the latter, but generally the stand is too open. In the desert plains, the bunch habit is more pronounced and the total production usually less. Quite apart from the question of yield, however, is that of time of development and ability to cure on the ground. From this

standpoint, the mixed prairie of tall *Stipa* or *Agropyrum*, and short *Buchloe*, *Bouteloua* or *Carex*, or the transition area of *Andropogon* and short grasses has a distinct advantage. The tall grasses either develop earlier or grow with such rapidity as to furnish the bulk of spring and summer feed, while the short grasses become cured in late summer to furnish feed for fall and winter. Finally, it must be recognized that the tall grass associations are agricultural indicators as well, and that economic considerations give them greater significance in this role. Our knowledge of the Sierran alpine meadow is too small to enable us to draw an accurate comparison with the Petran association. They are so nearly alike in the growth-form and genera of the dominants and in the number and luxuriance of the societies that they exhibit no clear difference in yield per unit area. In spite of this, the Petran association is actually very much more important, for it covers an area many times greater, is more coherent, and for the most part covered by snow to a less degree and for a shorter period. (Plate 26).

Local Grazing Types.—While the main grazing types, such as the formation and association, indicate the comparative value of great regions, as well as the groupings possible in any one, it is the local groupings which determine the grazing capacity of a particular ranch and the proper system of management to be employed upon it. For this reason, they may well be termed practical grazing types. In areas relatively uniform, a single grazing type composed of the two or three major dominants of the association may cover a wide extent. This is the case with *Stipa* and *Bouteloua* in North Dakota and Montana, *Buchloe, Agropyrum* and *Bouteloua* in the region of the Black Hills, and *Buchloe* in Oklahoma and Texas. As a rule, however, changes in topography or soil or in the number and grouping of the subdominants bring about important changes every few miles, and very frequently adjoining sections will be found to have a different grouping or an effective difference in relative abundance. Hence, it is clear that the local community must determine the careful classification of the land, section by section, especially with reference to grazing capacity, as well as the method of management. For example, while all the climax groupings in the mixed prairie resemble each other in structure and treatment much more than they do groupings of the true prairie, they show decisive differences among themselves. The grazing capacity and relation to overgrazing of the *Stipa-Bouteloua* community differ from that of *Agropyrum-Buchloe* and both of these

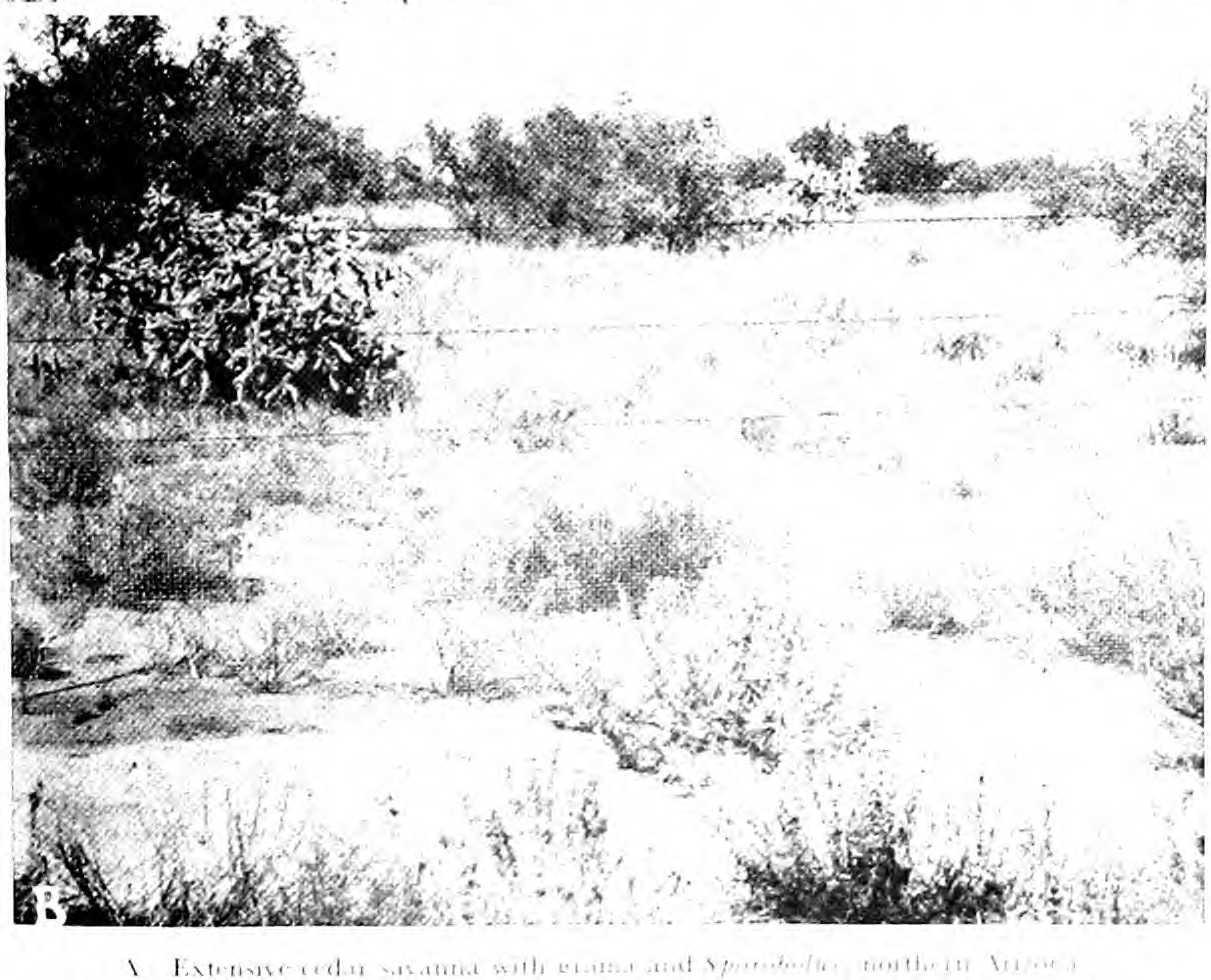


A. Mixed prairie of mid grass (*Agropyrum*) and short grass (*Bulbilis*), Winner, South Dakota.

B. Pure turf of short grass (*Bulbilis*), Ardmore, South Dakota.

from that of *Buchloe-Agropyrum-Bouteloua*. The marked development of societies reduces the abundance of the dominant grasses, and at the same time affects the grazing capacity. The relation between the two effects depends upon the degree to which the subdominants are grazed, but as a rule, they are less palatable than the grasses. Over regions of rolling topography, such as prairies and sandhills, the climax groupings are regularly interrupted by valley and ridge communities which are successional in nature. These are of relatively small extent and may frequently occur with the climax grouping on a ranch of a section or less in extent. In the case of the more level plains, the seral communities are confined to stream valleys and breaks and cover much larger areas. They often serve to mark the distinction between valley and upland ranches. They are not confined to one association, but such a grouping as that of the *Andropogons* may be found repeatedly from the true and mixed prairies through the desert plains.

Savanna as an Indicator:—Throughout the present treatment, the word savanna is used for the community which characterizes the ecotone between two climax formations. In its most typical expression, it consists of grasses and low trees or tall shrubs, and occurs in the hot, dry regions of the Southwest. Other communities are so similar that it is impossible to exclude them, and hence open pine forest and woodland with a grass cover are also called savanna. Closely related to these are the so-called natural parks of the Rocky Mountains in which seral grassland is surrounded and more or less invaded by trees. Such parks occur in both the montane and subalpine zones. When the ecotone lies between forest or woodland and scrub, the general ecological relations are similar to those of savanna, but the grassland is replaced by sagebrush, chaparral, or desert scrub. The trees stand more or less scattered in the scrub, and the indications of the community are primarily those of the latter. The failure to recognize this similarity to savanna has led to confusion with reference to the distinctness of the scrub climaxes in rough regions where they are interspersed with trees. Savanna has been so generally linked with the presence of grasses that it seems unwise perhaps to broaden its meaning to include areas of scrub with taller trees, and consequently the word park has been used for the latter. Thus, a sagebrush savanna is one in which sagebrush is scattered through grassland, while a sagebrush park is a community in which sagebrush is surrounded and more or less invaded by trees or tall shrubs.



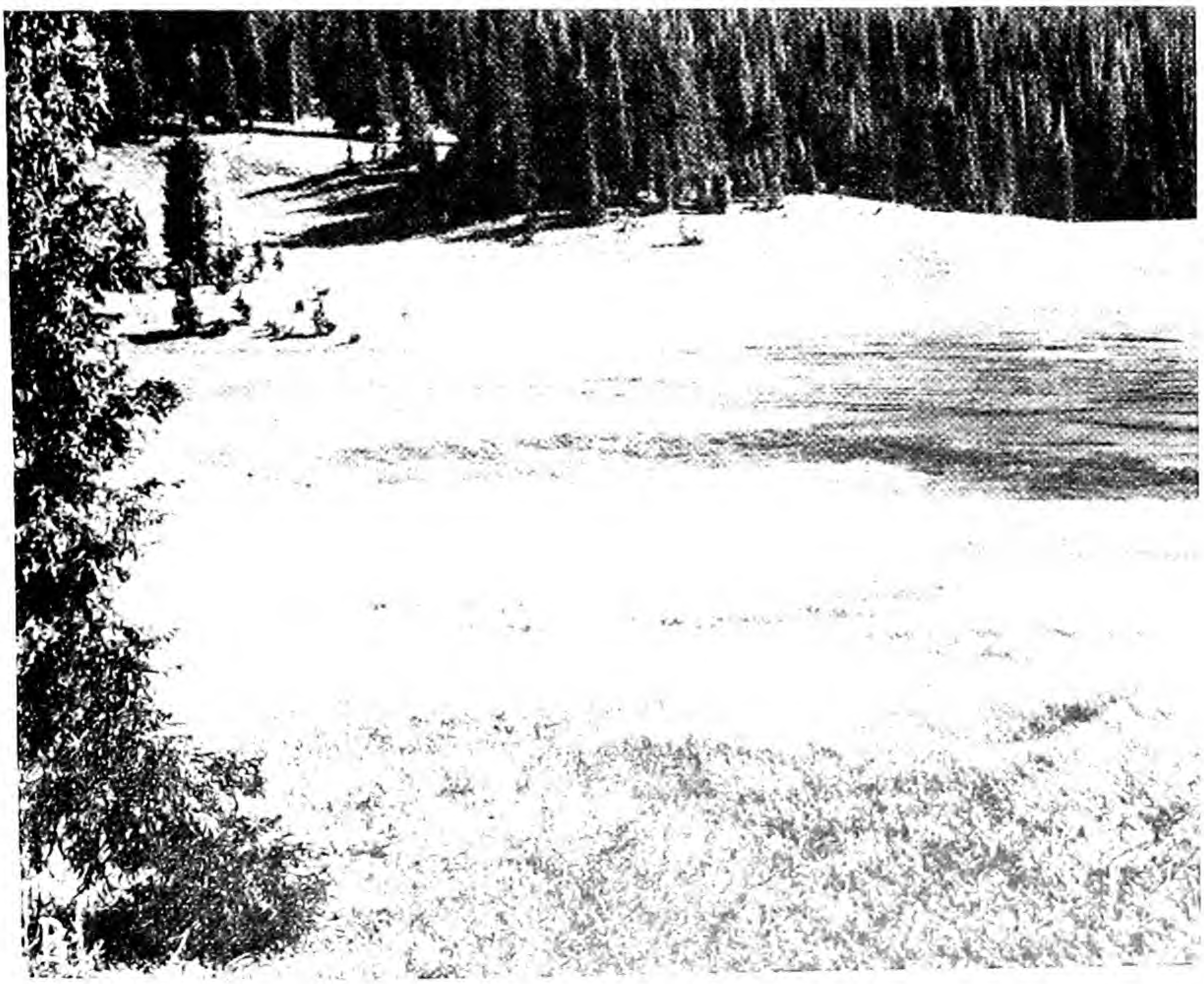
A. Extensive cedar savanna with grama and *Sporobolus*, northern Arizona.

B. Typical scrub savanna of mesquite, yucca, *Bouteloua* and *Aristida*, southern Arizona.

In their typical form, both savanna and park are controlled by the grasses or scrub, and the trees are more or less incidental. The transition to forest or woodland is usually gradual, and it is impossible to draw a sharp line between the two. However, it is a simple matter to distinguish the general areas from each other. As long as the trees or shrubs are far enough apart so that their shadows do not touch, the grassland or scrub remains in control. When they are sufficiently close to have their shadows overlapping during most of the day, the grass or scrub dies out for lack of sun, or persists only in small groups of much modified individuals. Tree and scrub savanna often cover extensive areas to which they give the appearance of open woodland, but the true nature of the community is indicated by the continuous carpet of grass, which serves as the indicator.

The indicator significance of savanna or park naturally depends upon the kind and the region, as well as upon the dominants. The best examples of tree savanna are to be found along the line of contact of forest or woodland with grassland. Oak savanna is the most common, occurring typically in central Texas, in Arizona, New Mexico, and Mexico, and in California and Lower California. Savanna in which yellow pine is the tree is frequent along the lower edge of the montane forest, where it extends out upon plateaus or plains. It is well-developed in northern Arizona and New Mexico, but is most extensive on the low ranges and high plains east of the central Rockies and around the Black Hills. Both pinyon and cedar form savanna, but the latter is much more frequent and extensive (Plate 27A). Typical scrub savanna is largely confined to the Southwest, ranging from Texas through southern New Mexico and Arizona, and northern Mexico. Its most characteristic shrub is mesquite, *Prosopis juliflora*, but *Yucca*, *Acacia*, *Ephedra* and other dominants of the desert scrub occur frequently (Plate 27B). Owing to its habit of growing in clumps or groups, chaparral tends to form grassy parks rather than typical savanna, especially along the edge of the Petran association. Sagebrush extends into several of the grassland associations to form what is essentially sagebrush savanna, though its low stature tends to obscure the exact relation. This is especially true where it meets the tall grasses, as in Wyoming and Oregon, but the savanna nature is obvious where tall sagebrush is scattered through short grass, as in southeastern Utah.

Parks differ from savanna chiefly in that the two communities concerned mix by alternating groups or areas rather than by scattered indi-



A. Oak savanna (Q[illegible]), Clear Lake, California.
B. Grass park in subalpine spruce, Colorado.

viduals. Excellent examples of grass parks occur in the subalpine forests of Colorado, where spruce and balsam enclose extensive meadows of *Festuca*, dotted with groups of young conifers or aspens. Somewhat similar parks occur at timberline, where the forest breaks into groups which extend well up into the alpine meadows. Sagebrush parks occur most commonly in the lower subclimax portion of the woodland zone, while sagebrush areas dotted with groups of lodgepole-pine or aspen are frequent on the western slope of the Rocky Mountains in Colorado and Wyoming. Chaparral parks are best developed in California, especially in the case of subclimax chaparral in the pine forest and where the climax type meets the pine-oak woodland. In the Rocky Mountain region they occur chiefly as scrub openings in the pinyon-cedar or oak-cedar woodland.

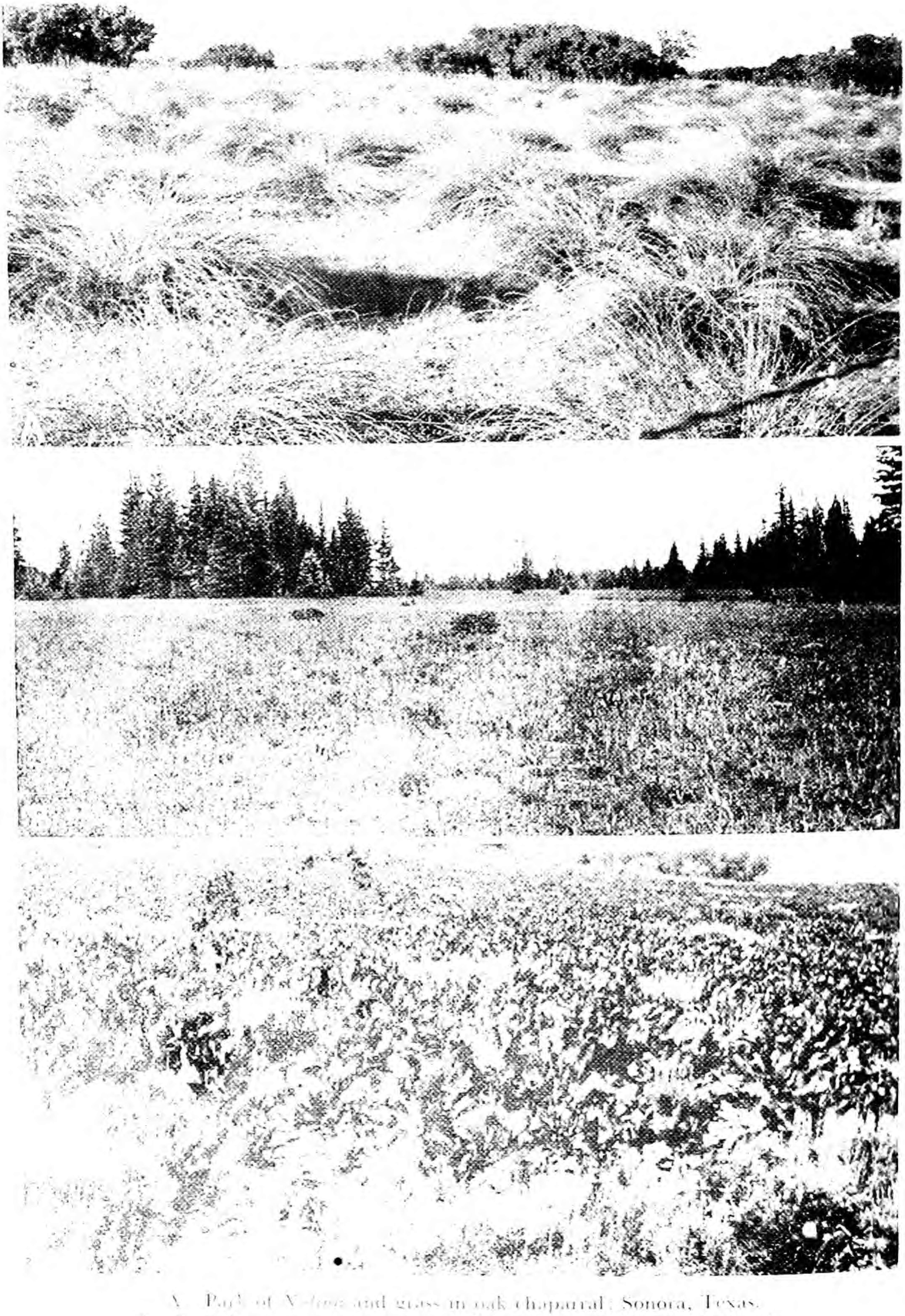
Savanna and park are alike as indicators in that they denote a transition from one community to another. They differ for the most part in that savanna is an indicator of climate, and park usually of local or edaphic conditions. Savanna has to do with the relations of two contiguous climaxes, and park with that of a subclimax to its climax. The former is a permanent condition, varying more or less under the influence of the wet and dry phases of climatic cycles, while the latter is usually a temporary community, occupying its proper place in prisere or subsere, and passing ultimately into the climax. True savanna has value as an indicator of climate as well as of practice. It not only indicates a transition between the climates of the respective climaxes, but also serves to record the course of the climatic cycle. The amount to which it increases its area and density under the same conditions is a measure of the effect of the wet phase, and the dying-out of individuals, of the dry phase. Such measurements are possible only under control, however, owing to the almost universal disturbance of fire or overgrazing (Plate 28).

Savanna in Relation to Fire and Grazing.—The general view in the Southwest is that mesquite and oak savanna are limited or destroyed by fire and that they have spread rapidly in recent years, since the annual burning has ceased. In the absence of definite measurements, many of the statements can be accepted only in part, though the general relation to fire seems evident enough. Tree savanna appears to be affected little by burning, except that this must have been a powerful factor in spreading the annual *Avena* in California at the expense of the perennial *Stipa*. The effect of fire upon scrub savanna depends upon a number of factors,

chief among which are density and height of both shrubs and grasses, the ability of the shrubs to form root-sprouts, and the frequency of fires. It seems certain that annual fires in scrub savanna that is densely covered with tall grasses would destroy the shrubs completely in a few years, no matter how great their ability to form root-sprouts. Less frequent burning of open savanna, in short grass especially, would damage the shrubs much less and might well increase their control by promoting root-sprouting. Moreover, in the more xerophytic grasslands, frequent burning during dry seasons injures the grass and would tend to favor the shrubs in consequence.

The general effect of grazing is to increase the shrubs at the expense of the grass. As has been seen, savanna owes its character to a dry climate in which the ecesis of shrubs is regarded as usually possible only during the wet phase of the cycle. This means that shrubs and grasses live constantly under keen competition for water, and that anything that reduces the amount of grass will be to the advantage of the shrubs. Since grasses and forbs are usually eaten to a much larger degree, intensive grazing, and especially overgrazing, will reduce their hold upon the soil and correspondingly improve conditions for the spread of shrubs. The seeds of the mesquite and other shrubs are widely scattered as a consequence of being eaten or through unintentional carriage, and the seedlings are more readily established in areas where the hold of grasses has been weakened. The local spread of the scrub clumps is chiefly by means of root-sprouts and is promoted by light browsing, but restricted by heavy browsing. Thus, while savanna is primarily an indicator of climate, its secondary indication is one of grazing and absence of fires, upon which its practical utilization must be based. This can be done readily only after plant measurements have made clear the exact behavior of savanna under different methods of burning and grazing (Plate 29).

Significance of Seral Types.—While seral communities are temporary in comparison with climax ones, many of them persist for tens or even hundreds of years, and in actual practice may be regarded as permanent. The majority results from disturbance, however, and lasts for a period of a few years, or at most for a decade or two, unless the disturbance is continuous or recurrent. In addition, such communities show rapid changes of population from year to year, are usually local and of small extent and have resulted from fire, overgrazing or cultivation. They belong to secondary successions or subseres in contrast to the larger and more perma-



A. Park of *Nolina* and grass in oak chaparral; Sonora, Texas.
B. Burn Park in subalpine forest; Uncompaghre Plateau, Colorado.
C. Burn Park of *Wyethia* and *Artemisia* in chaparral; Logan, Utah.

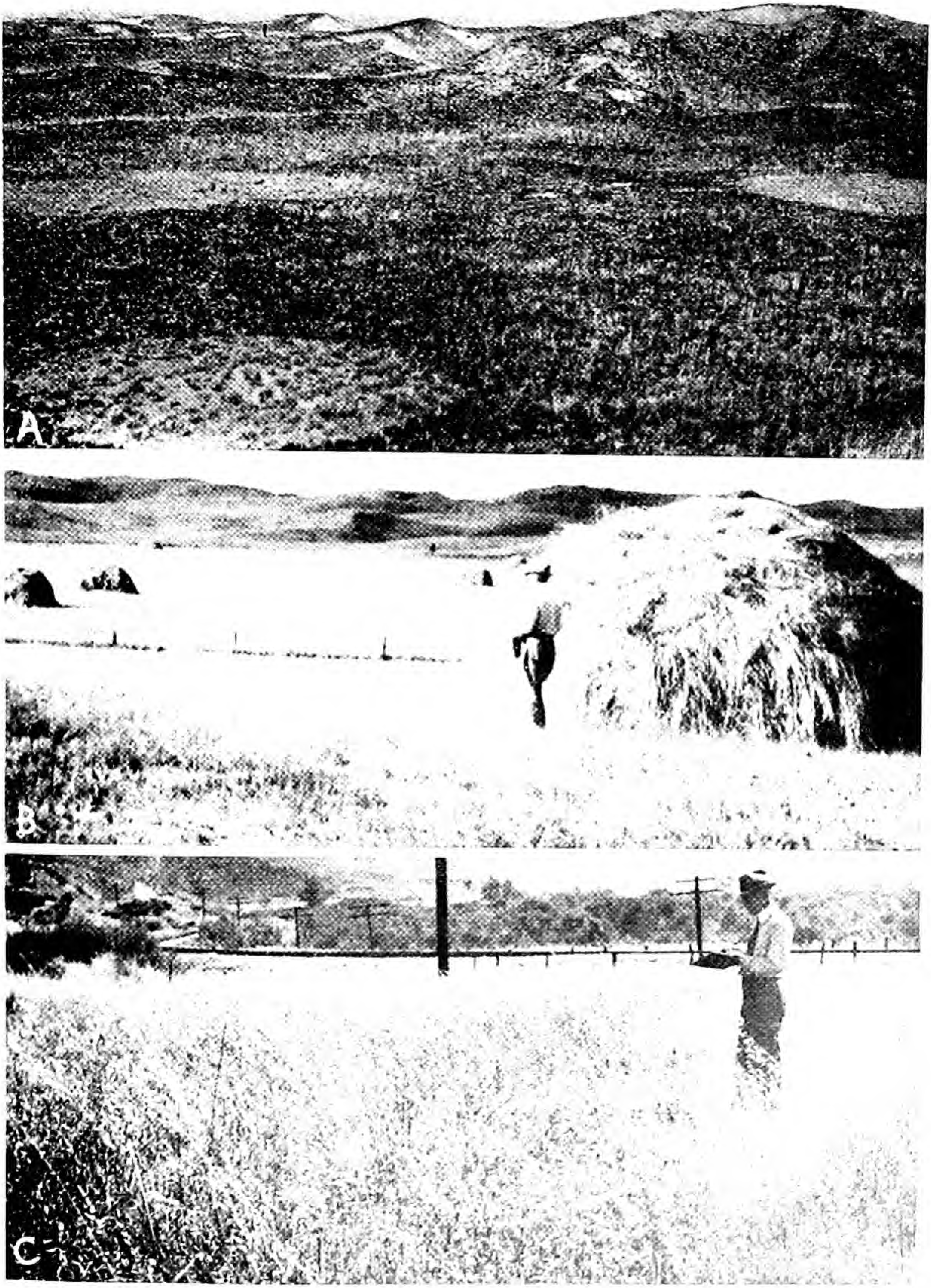
nent communities which constitute stages in the primary succession or prisere. These distinctions apparently disappear in the case of great stretches which are kept more or less permanently in the lodgepole or aspen community as a consequence of repeated fires, or in the *Aristida* or *Gutierrezia* stage as a result of continued overgrazing. Even here, however, the differences in the kind and rate of development are of great practical value in determining the proper management. As a consequence, it is desirable to distinguish seral communities as indicators upon the basis of primary and secondary succession, and then to deal with the indicator value of the respective dominants. Each of these is known as a consocies when it is controlling, and corresponds with the consociation among climax types. Two or more consocies regularly occur together to constitute a particular stage or associes, while their subdominants are known as socies, which correspond to the societies of climax communities. A complete treatment of seral indicators is neither possible nor desirable at present, but the following account will serve to illustrate all the important types.

Prisere Communities as Indicators.—The four great types of primary succession are those which start in initial bare areas of water, rock, dune-sand, or saline lake or basin respectively. The initial communities and some of the medial ones may be used as negative indicators, denoting that conditions have not reached the point where they can support a plant cover of such density or quality as to furnish grazing. The later communities, and especially the subclimax one that immediately precedes the climax, form a more or less complete cover in which grasses or shrubs are usually in control. The density of the cover and the quality of the grazing increase more or less regularly from the medial stages to the climax, and the position of a particular community in the sere indicates its value in a general way.

The most important seral indicators of grazing are the later stages of the priseres in dunes and sandhills, in badlands and in salt basins. These often cover many thousand square miles and frequently occur in agricultural regions, where the indicator distinction between grazing and farming land is especially important. In addition, there are the sedge and grass meadows which are stages of the hydrosere, and are often characteristic of mountain parks in the montane and subalpine zones. Grassland and scrub also develop in rock fields and on talus slopes where the formation of soil is not too slow. While such parks and gravel-slide areas

often afford excellent grazing, they are usually both local and relatively small and serve chiefly to increase the grazing value of the forest areas in which they occur.

Of all the prisere communities, those of sandhills and dunes are probably the most widely distributed and most important. They have been found and studied in each of the 16 Western States, where they may occur as sandhill regions of large extent, as river dunes or ocean dunes. The most extensive sandhill areas occur in Nebraska, Kansas and Colorado, though they are scattered throughout the grassland climax from North Dakota to Texas and New Mexico. Such areas differ from dunes chiefly in extent and complexity, and in the fact that they are no longer connected with an active shoreline from which the sand is derived. They are essentially stable dunes with blowouts as characteristic features, and for the most part they exhibit subclimax communities. The succession in sandhills and dunes is practically identical for the same climax, but differs greatly between climaxes, especially in the later stages. The largest and most important sandhill region is that of central Nebraska, which covers an area of about 20,000 square miles. It has received much study during the past fifty years, and the ecological results have been summarized in bulletins and monographs of the university. The typical community of the sandhills is the bunch grass subclimax, consisting of *Andropogon hallii* and *A. scoparius.* The blow-sand condition, typical of blowouts especially, is indicated by *Redfieldia, Psoralea,* and *Petalostemon,* which have little or no grazing value. More stable conditions are denoted by *Muhlenbergia* and *Calamovilfa,* and these are correlated with increasing grazing value. The next stage is that of the *Andropogon* subclimax, which possesses a much higher value. By the entrance of *Stipa* and *Koeleria,* the subclimax passes into the true prairie, while in the western portion the invasion of *Bouteloua* and *Buchloe* indicates the appearance of the short grass subclimax, or of mixed prairie when *Stipa* and *Agropyrum* occur also. The hydrosere is a regular feature of the innumerable wet valleys and of the extensive lake region. The first community to indicate grazing is composed of rushes and sedges, and this changes slowly into the typical meadow associes of *Agropyrum, Andropogon, Elymus, Panicum* and *Spartina,* which is essentially an extra-regional portion of the subclimax prairie. The grazing value of such a group of dominants is obvious, but in practice such meadows are used for hay, since the hills furnish summer grazing (Plate 30A and B).



A. Seral stages of subclimax grasses, *Andropogon* and *Calamovilfa*, in the sandhills, indicating grazing, Halsey, Nebraska.

B. Grass meadows in the sandhills, used for hay, [illegible], Nebraska.

C. Disclimax of annual *Avena* and *Bromus* produced from prairie [illegible], San Fernando Valley, California.

Like the sandhills, badlands are found throughout the West. Massive badland complexes are most typical of the states which touch the Black Hills, but they are frequent also in practically all those along the Rocky Mountain axis, while outlying areas of much interest are found in Texas, Oregon and California. The actual communities of the sere likewise differ with the climax. The two most important seres are the xerosere of the Tertiary badlands in the Great Plains region of the grassland climax, and the halosere of the Great Basin. The former possesses a number of herbaceous stages which have an increasing value for sheep-grazing as they become denser, but grazing proper is indicated only when *Agropyrum* becomes abundant. *Bouteloua* and sometimes *Buchloe* also enter somewhat later to form a mixed prairie, and the latter then becomes definitely constituted by the appearance of *Stipa*. The lower valleys are often controlled for a time by sagebrush, but this ultimately yields to the grasses. The juxtaposition of weed, grass, and sagebrush types indicates the value of badland areas for mixed grazing, and suggests the importance of hastening the course of succession in them. The badlands of the sagebrush disclimax are characterized in the initial stages by colonies of halophytic annuals, which have some grazing value where they make a definite cover. The first stage of much importance is formed by the low perennial species of *Atriplex*, such as *A. nuttali*, *A. corrugata*, and *A. pabularis*. These are followed by *Atriplex confertifolia* and *Grayia*, and these are finally invaded by *Artemisia tridentata* to form the mixed or pure grazing type so characteristic of the Great Basin and its outlying regions. In the badlands of the Painted Desert in northern Arizona, the general course of the sere is much the same, but the grasses replace *Atriplex*. The normal sequence in the subclimax stages is the replacement of *Sporobolus airoides* by *Hilaria jamesi*, and this by *Bouteloua*, often with *Muhlenbergia* also. The course of development in the halophytic badlands is essentially a part of the widespread succession in saline basins, except that the latter often begins in water. Shantz has indicated the course of the succession in detail, and it must suffice to point out that the first important indicators of grazing are usually scrub dominants, *Sarcobatus* and *Atriplex* (Plate 15C). Some of the playas of the Southwest are intensely saline, and show essentially the same communities, but the majority are secondary in nature and belong to the subsere.

Subsere Communities as Indicators.—Subseres are developed in sec-

ondary areas, such as are regularly produced by fire or cultivation. They occur also in other bare areas in which the disturbance is not sufficient to destroy the soil or to make extreme conditions for ecesis. They are a constant feature of overgrazing and a normal consequence of the presence and activity of man. They are usually local and of small extent, but in the case of fire they may occupy hundreds of square miles. The successional movement is normally rapid, but its progress may be slowed or stopped by the recurrence of the disturbing agency. When this is the case, the area concerned may be held more or less permanently in a subclimax or other seral stage. The most important and extensive subseral communities are those due to fire. The consequences of overgrazing often cover great stretches, but the actual communities change more or less, or they are much interrupted. Those due to cultivation are usually confined to fields, though many of the dominants become extended to roadsides, and some even enter the natural vegetation. While they often have grazing value, it is incidental and temporary and their chief value lies in connection with utilization as supplementary forage crops, as already indicated for *Salsola, Helianthus, Melilotus*, and others.

Certain grasses, such as *Poa, Avena*, and *Bromus*, have become widespread dominants as a consequence of the combined action of two or more agencies. In the case of *Avena* and *Bromus*, the species concerned, *A. fatua, B. tectorum, B. rubens*, etc. are annuals which have replaced the native dominants as a general result of the combined effect of overgrazing and fire. As annual grasses, these should have a low grazing value, but this is much less true of *Avena* than of *Bromus*, owing largely to the difference in size and habit. Even *Avena* is less valuable than the native perennial grasses which they usually replace, and this suggests the desirability of taking advantage of the principles of succession to restore the original community where it has not been completely destroyed (Plate 30C). *Poa pratensis* as a perennial grass of meadows has practically the same ecological habits and grazing value as the prairie dominants which it replaces. Its rapid spread in the valleys and ravines of the true prairies seems to have been the result of a certain amount of disturbance, but *Poa* is not a true seral consocies, such as the annual *Avena* and *Bromus*. Among other such consocies of importance are *Plantago patagonica, Portulaca oleracea, Boerhavia torreyana*, and *Polygonum aviculare*. These are all indicators of disturbance, particularly overgrazing, but in the green condition they also have more or less value as indicators

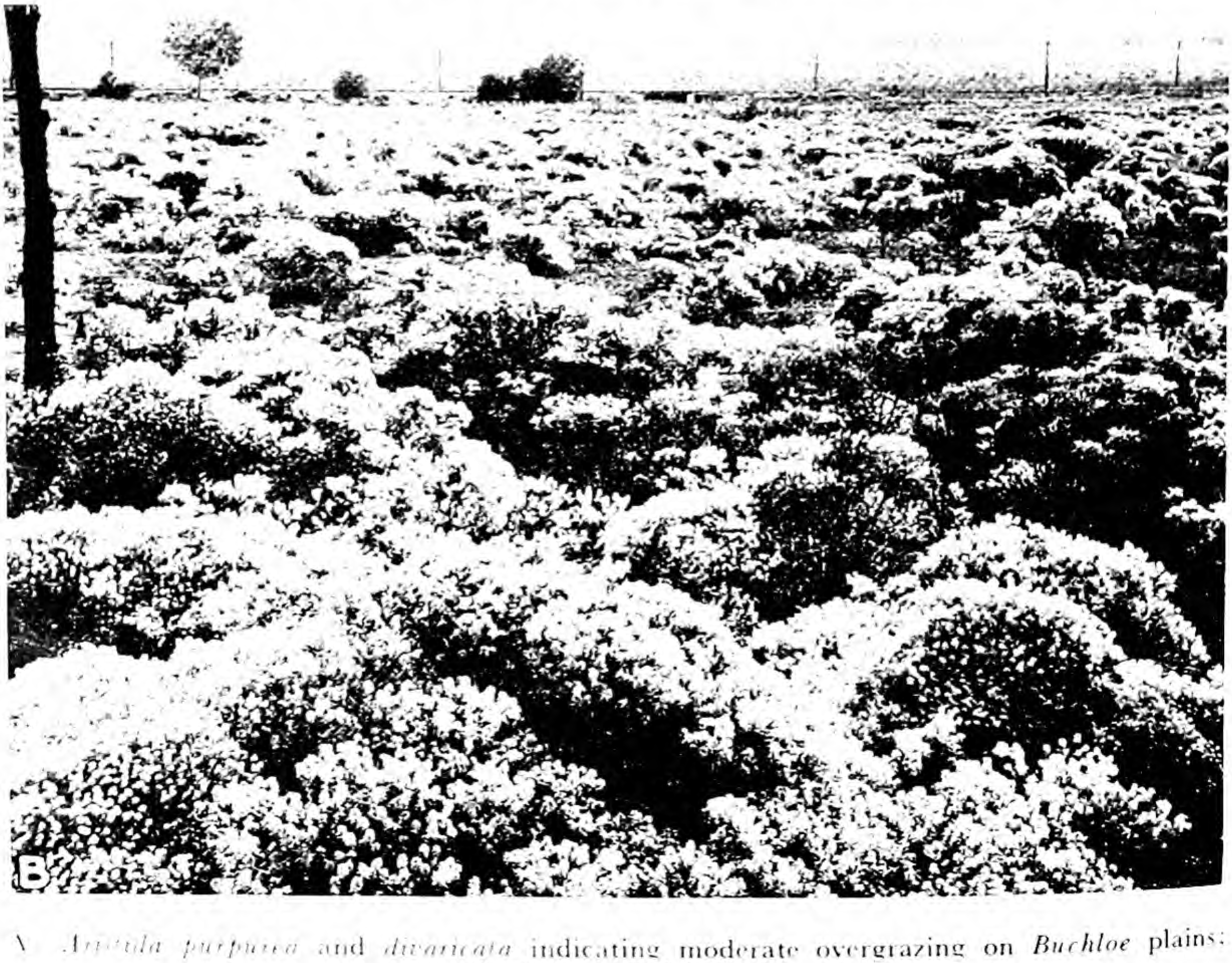
of an available weed type. Other indicators of disturbance are represented by such plants as *Hilaria mutica, Scleropogon brevifolius, Franseria* and *Buchloe*. These occur in playas or "swags" which are subject to flooding and in which a thin annual layer of silt is often deposited as well. The first two are commonly associated, partly owing to the fact that the disturbance of the *Hilaria* consocies by trampling and overgrazing favors the spread of *Scleropogon*. Tobosa swags are typical seral areas in the desert scrub as well as in the zone of savanna which lies between this and the desert plains. In the latter particularly, *Hilaria* is a characteristic subclimax, in which *Scleropogon* is usually an indicator of grazing disturbance, frequently with a similar associate, *Sporobolus auriculatus*. *Hilaria* is an indicator of summer grazing, while the other two are rarely grazed except under drouth conditions. The playas of the southern Great Plains are marked by a similar subsere, in which *Franseria* is the important early stage and *Buchloe* the subclimax. Both of these are grazing indicators, though the value of the *Franseria* is relatively small.

Fire Indicators and Grazing.—The typical indicators of fire are trees and shrubs, and they may have a direct or indirect relation to grazing. The indicators may themselves be browsed, or they may be associated with layers of herbs or shrubs which furnish feed. Grasses and other herbs may indicate fire, but are usually associated with woody indicators or their relicts. The most important "burn" communities are pine forest, aspen woodland, chaparral, and savanna. In addition, there are grass and sagebrush parks which also represent subseres initiated by fire. Savanna has already been considered, while the grazing value of grass parks is obvious. Sagebrush and chaparral are primarily browse types, though they contain a larger or smaller amount of grass or forbs as well. When young, aspen woodland furnishes a large amount of browse, but it is chiefly valuable for the more or less luxuriant ground cover. This changes with the course of succession from firegrass, fireweed and other pioneers, to the characteristic mixed layer communities of the mature aspen subclimax. The latter exhibits three chief grazing types, forb, grass, and shrub, of which the first is most common and the second the most valuable. The pine communities which regularly indicate burns are lodgepole and knobcone forests. The subclimax of lodgepole, *Pinus contorta*, is much the most extensive and important, occurring in both the montane and subalpine zones of the Petran and Sierran regions. The

community of knobcone pine, *Pinus attenuata*, is a similar fire subclimax, but it is confined to southern Oregon and California. In the Rocky Mountains, the mature lodgepole forest is almost completely without a ground cover, and hence possesses almost no grazing value. In its earlier stages, forb and grass associes are well-developed, and for a time aspen scrub may form a typical stage. In the Coast forest, *Pseudotsuga* and *Larix* are fire indicators and their communities exhibit forb and shrub layers in the early stages especially.

4. Overgrazing

Nature.—In practice, a range is regarded as being overgrazed only when its grazing capacity is actually decreased. Such a test is often indefinite because of the conditions under which the stock industry is carried on, and this explains the divergent views as to the condition of particular ranges. While conclusive evidence as to the degree of overgrazing must be obtained from the failure of a range to maintain the herd upon it, such evidence can rarely be secured except from experimental tests. This is due to many factors, of which variation in capacity with the climatic cycle and differences in management are the most important. As a consequence, it is most satisfactory to draw evidences of overgrazing from the behavior of the plant cover and to determine the degree by means of quadrat and other measurements. The competition between the individuals and species of the plant community is so keen and the balance so exact that the slightest disturbance can be readily detected. Grazing itself constitutes such a disturbance, and its effects upon growth, propagation, and reproduction can be accurately determined. Such dominants as the grasses, however, have a marked advantage over the subdominant forbs because of their underground parts and methods of growth, so that only a severe disturbance can throw the balance in favor of the forbs. When this happens, the first evidence is afforded by the increase in the number and vigor of the latter, which consequently serve as indicators. With increasing disturbance due to overgrazing, the annual members of the native flora appear in the most disturbed areas as the pioneers of minute subseres, and are later followed by introduced weeds. In the final condition the grasses will have disappeared, largely or completely, only the more weedy societies will persist, and the ground will be chiefly or wholly occupied by weedy annuals and biennials. Such a community represents one or more stages of the secondary succession and its



A. *Aristida purpurea* and *divaricata* indicating moderate overgrazing on *Buchloe* plains; Texhoma, Oklahoma.
B. An annual, *Lepidium alyssoides*, indicating complete overgrazing in a pasture; Fountain, Colorado.

tenure depends upon the continuance of the disturbance that initiated it. If the latter ceases, the successional process begins and soon terminates in the original climax if the grass dominants have not been killed out. Under these conditions, succession is universal and inevitable in all climaxes, and this fact is essential to all methods of range improvement.

On the basis of the maximum annual production of forage, overgrazing occurs whenever the yield drops below this point. It is evident that the maximum production cannot have a fixed or average value, but that it must be correlated with the periods of the climatic cycle. A degree of grazing that would be disastrous in a drouth period would fall far short of adequate utilization during a wet one. Coville has applied the term "destructive overgrazing" to the condition in which all or part of the native dominants are killed. It is characteristic of areas overgrazed during the critical drouth periods of the double sun-spot cycle. Overgrazing results when the proper maximum yield of a particular year or period is not obtained because of the failure to make enough food for propagation or seed-production, or because the seed-crop has been destroyed. There are varying degrees of overgrazing from a slight reduction in yield to the complete destruction of the range. Close grazing is the type in which the total annual yield is utilized in such a way as to maintain the grazing capacity (Plate 31).

Causes.—The primary cause of overgrazing is stocking the range with more animals than it can carry and still maintain its annual yield. This has been the universal method by which the stockman has maintained a title to his portion of the open range, since an overgrazed range offered little attraction to a new-comer. Overstocking has become such a general practice throughout the West, on private lands as well as upon the open range, that stockmen have almost completely lost sight of the potential grazing capacity of their ranges. A corollary of this is the practice of year-long grazing or of grazing during too long a season, with the result that the grass does not make a proper growth in the spring or fails to ripen and drop its seeds in the fall. Trampling is an inevitable concomitant of overstocking and frequently does more damage than the actual grazing, especially in the vicinity of wells and tanks. In addition, there are several important contributary causes of overgrazing. The most important of these is the drouth period of the climatic cycle. The general practice of stockmen takes too little account of the great variation in yield between the dry and wet phases. The interval between them usually per-

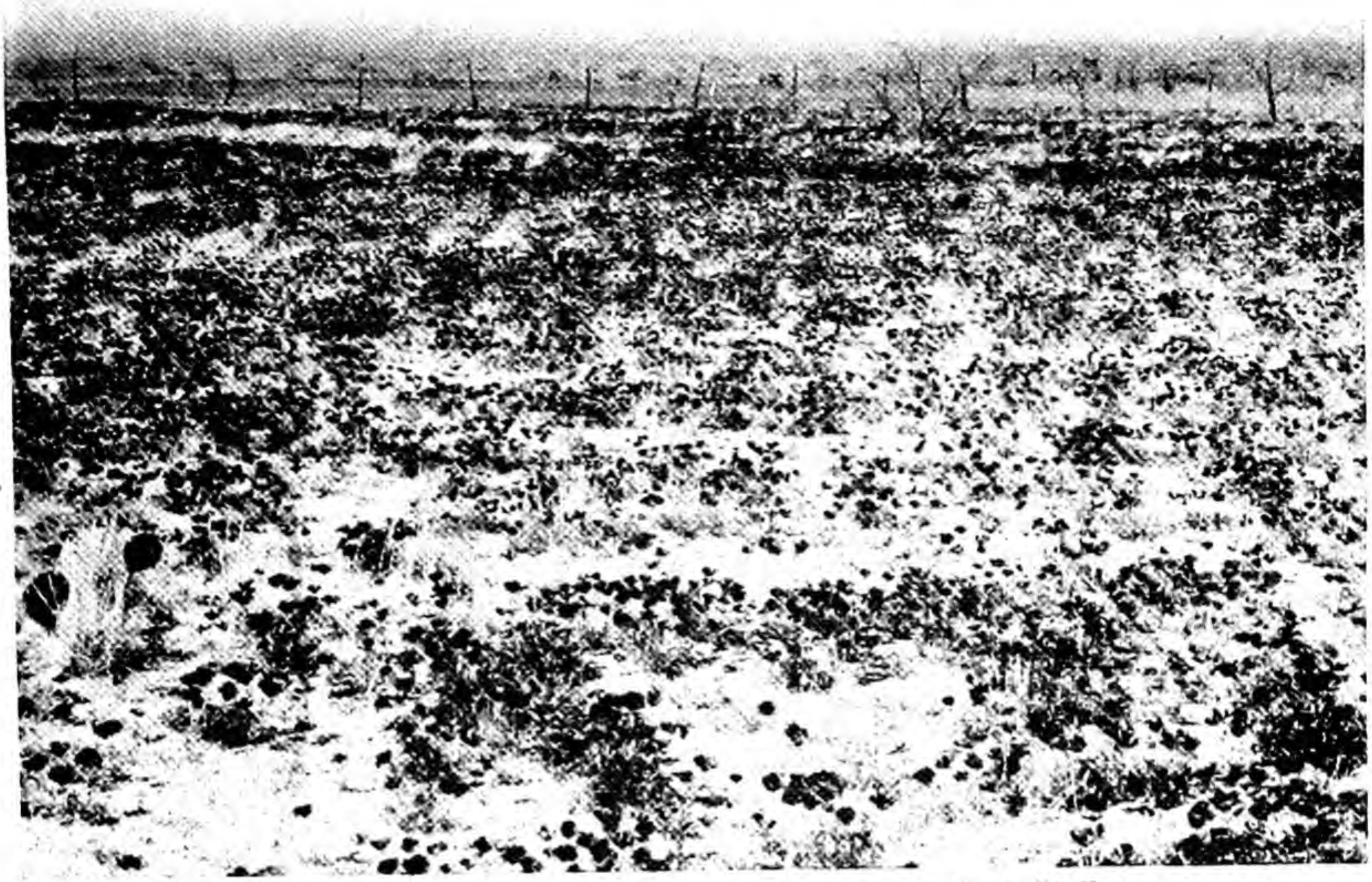
A. *Aristida-Bouteloua* association in 1917; Santa Rita Reserve, Tucson, Arizona.
B. The same area in 1918 after serious drought and overgrazing by cattle and rodents.

mits the building up of the herd to the point where the range cannot carry it during the dry phase. For a year or more the range is destructively overgrazed, until the herd is moved or a large portion has died. During such drouth periods as those of 1893-95, 1916-18, and 1931 to 1936, the range was so damaged as to require several years to regain a fair grazing capacity and many years to permit the development of its potential capacity. The effect of rodents upon the range is essentially a matter of over-stocking. A range which is carrying thousands of prairie-dogs or jack-rabbits is in effect already stocked with a considerable number of cattle. In the usual practice, however, no allowance is made for this fact, and the rodents steadily increase the damage done by the prevailing overstocking with cattle. This double effect becomes most disastrous during the drouth period and frequently results in the complete destruction of the range over large areas, especially in the Southwest. The effect of fire upon the range is relatively unimportant by comparison, but it does sometimes do serious damage to the mixed prairie and desert plains by killing the rootstocks, particularly during dry seasons or dry years (Plate 32).

Indicators of Overgrazing.—In grassland and scrub practically every species may serve as an indicator of overgrazing. This is true also of forbs and shrub associes, especially those of the subsere. In the case of woodland and forest the dominants can act as indicators only in the seedling or sapling stage, but the forbs and shrubs may indicate overgrazing as clearly as in other communities. The primary basis of overgrazing indicators lies in the fact that at any particular stage some species are eaten and others not. Thus, at any time the degree of overgrazing can be determined from both sets of plants. The best method consists in using one set as positive indicators of excessive grazing, and the other as a check upon these results; but in actual practice the most convenient indicators are naturally those that are not eaten. In any community such relict indicators owe their importance in the first place to the fact that the more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. They receive a progressively larger share of water-content and light, and their growth increases accordingly. This leads to greater storage in the propagative organs as well as to larger seed-production. At the same time, the grazed species are correspondingly handicapped in all these respects, and the gap between forbs and grasses,

for example, constantly widens. With the increase of the less palatable species, especially when they are bushy, the grasses are further weakened by trampling. This soon produces small bare spots which are colonized by annual weeds or weed-like plants. The latter set up a new and intense competition with the grass survivors, and these are still further decreased as a result. The weed areas widen, and sooner or later come to occupy most or all of the space between the relict forbs or half-shrubs. Before this condition is reached, however, the latter are brought into requisition for grazing and they then begin to yield to the competition of the annuals. In the case of the severest overgrazing, they too finally disappear, unless they are woody, wholly unpalatable, as in *Gutierrezia,* or thoroughly protected by spines, as in *Opuntia.*

In the mixed prairie climax, where the effects of overgrazing have been most studied, it is possible to recognize three or four stages. The first is marked by the decrease or disappearance of *Stipa* or *Agropyrum,* or of both of them, and the corresponding increase of the short grasses wherever these are associated; the second stage is characterized by the greater vigor and abundance of the normal societies, as well as by the increased importance of some; the third stage begins with the replacement of the grasses by annuals, while the fourth is marked by the spread of annuals and of introduced weeds generally over the area. Not all of these necessarily occur in the same spot, especially when the process of overgrazing takes place rapidly. Destructive overgrazing may result in a few years, or even in a single year, and in such instances the native vegetation may disappear completely or nearly so. It is replaced by a pioneer associes of native and introduced weeds, whose persistence will depend upon the continuance of the disturbance. These four stages indicate so many primary degrees of overgrazing, while minor degrees are denoted by the dropping out of particular dominants or subdominants. Thus in the mixed prairie, *Stipa* drops out before *Agropyrum,* because it is grazed more heavily in spring, and *Bouteloua* disappears from the desert plains before *Aristida,* owing to its greater palatability. Palatability is the chief factor in determining the successive disappearance of species, and hence the indicators of the corresponding degrees of overgrazing, though the sequence is often disturbed by the vigor of certain dominants. Since there are few species that are wholly unpalatable or inedible, it becomes possible to construct for a particular community a complete sequence of indicators, reflecting each appreciable degree in the process of overgrazing. In severe periods



Santa Rita Range Reserve, Tucson, Arizona

A. A winter annual (*Eschscholtzia mexicana*), indicating both overgrazing of grasses and grazing capacity.

B. Denuded area about a kangaroo-rat mound in the same area.

of drouth, overgrazing may reach the point where even the annuals are eaten out and the plant covering vanishes completely. This happens regularly in pastures, corrals and bedding-grounds where animals are kept in masses. It has even been found in desert scrub and savanna where the effects of overgrazing are supplemented by the work of kangaroo-rats (Plate 33).

Societies as Indicators.—The number of overgrazing indicators for the several climaxes is legion, and it is possible to consider only the most widespread and important. With the perennial grasses as a background, it is convenient to distinguish several groups of such indicators, namely, forbs, subdominant halfshrubs, cacti, seral annuals, introduced weeds and shrubs. The first three groups comprise the characteristic relict indicators, and for the most part mark the early stages of overgrazing. The annuals and weeds are typical of the later and final stages, while the shrub indicators are typical of savannas and other ecotones where grass and scrub mix. The increased importance of societies marks the beginning of overgrazing in those associations where they are regularly present. These consist for the most part of forbs of the climax, but subclimax halfshrubs and grasses, such as *Gutierrezia* and *Aristida*, are often of especial significance. Moreover, many of the forbs, though regularly present in the climax, have subclimax qualities also, as is readily understood from their competitive relations to the grasses. Practically all of the societies listed under the various associations of the grassland, as well as those of the other climaxes have some value as indicators of overgrazing. In most cases this value is overshadowed by that of the most controlling and extensive societies, and the latter alone need to be taken into account.

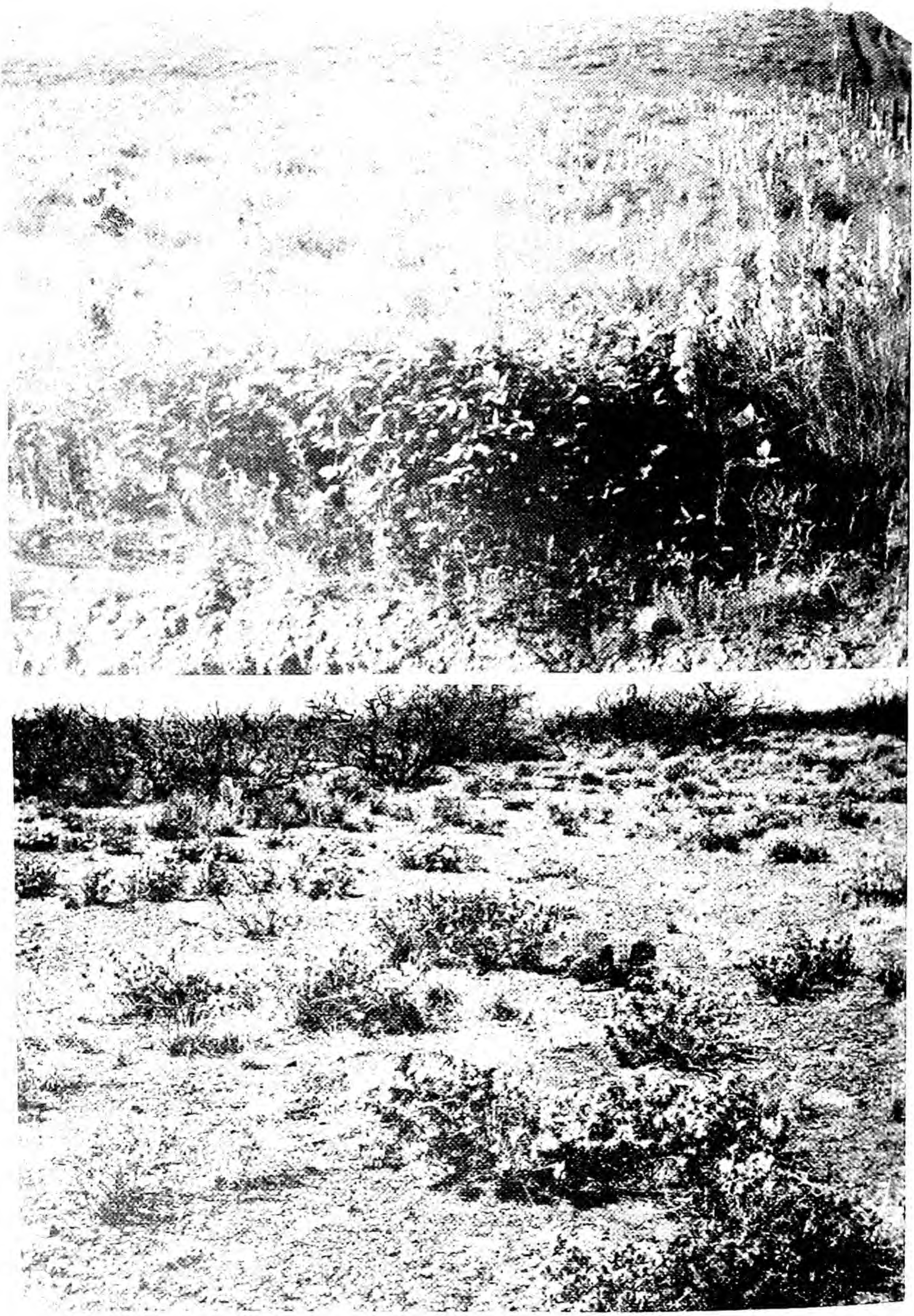
In the following list the general order is that of importance, but this naturally varies with the locality and the season. The composites and other late-blooming species are especially serviceable, owing to their persistence.

Artemisia gnaphalodes	Solidago canadensis	Kuhnia glutinosa
Artemisia dracunculoides	Solidago mollis	Malvastrum coccineum
Artemisia canadensis	Liatris punctata	Vernonia fasciculata
Grindelia squarrosa	Liatris scariosa	Vernonia baldwini
Solidago rigida	Liatris spicata	Achilleia millefolium
Solidago missouriensis	Liatris pycnostachya	Helianthus rigidus
Solidago speciosa	Lepachys columnaris	Carduus undulatus

Senecio douglasi	Tradescantia virginiana	Astragalus crassicarpus
Aster multiflorus	Verbena stricta	Lupinus plattensis
Aster oblongifolius	Verbena hastata	Erigeron ramosus
Aster sericeus	Glycyrhiza lepidota	Haplopappus spinulosus
Senecio aureus	Brauneria pallida	Hymenopappus tenuifolius
Balsamorhiza sagittata	Chrysopsis villosa	Rosa arkansana
Balsamorhiza deltoidea	Lygodesmia juncea	Euphorbia corollata
Psoralea tenuiflora	Aragalus lamberti	Salvia azurea
Psoralea argophylla	Polygala alba	Asclepias verticillata
Petalostemon candidus	Antennaria diocca	Monarda fistulosa
Petalostemon purpureus	Astragalus mollissimus	Baptisia leucophaea
Amorpha canescens	Astragalus bisulcatus	Castilleia sessiliflora
Amorpha nana	Astragalus racemosus	Allium canadense
Dalea laxiflora		

Halfshrubs as Indicators. — Halfshrubs are best developed in the Southwest, where they are typical indicators of overgrazing in both the desert scrub and the desert plains. A few attain even greater importance in the short grass plains and the mixed prairies. These are *Gutierrezia sarothrae*, *Artemisia frigida*, and *Yucca glauca*. The relation of the first two to grazing in a short grass cover has been shown by Shantz (1911:42). Over the central portion of the Great Plains they are associated as the two most serviceable and universal of overgrazing indicators. *Artemisia* is more abundant to the northward, and *Gutierrezia* to the southward, but they indicate essentially the same conditions whether alone or mixed. Differences in the degree of overgrazing are designated by variations in the density and vigor of the plants. In rough or sandy regions *Yucca glauca* is an indicator of overgrazing, though it is less important than the two just mentioned, largely because the flower-clusters are often eaten by cattle. *Eriogonum microthecum* and its variety *effusum* are common indicators in the central Great Plains, especially in more sandy areas or in sandhills. *Eriogonum jamesi* is even more frequent in a similar role, though it is barely shrubby (Plate 34A).

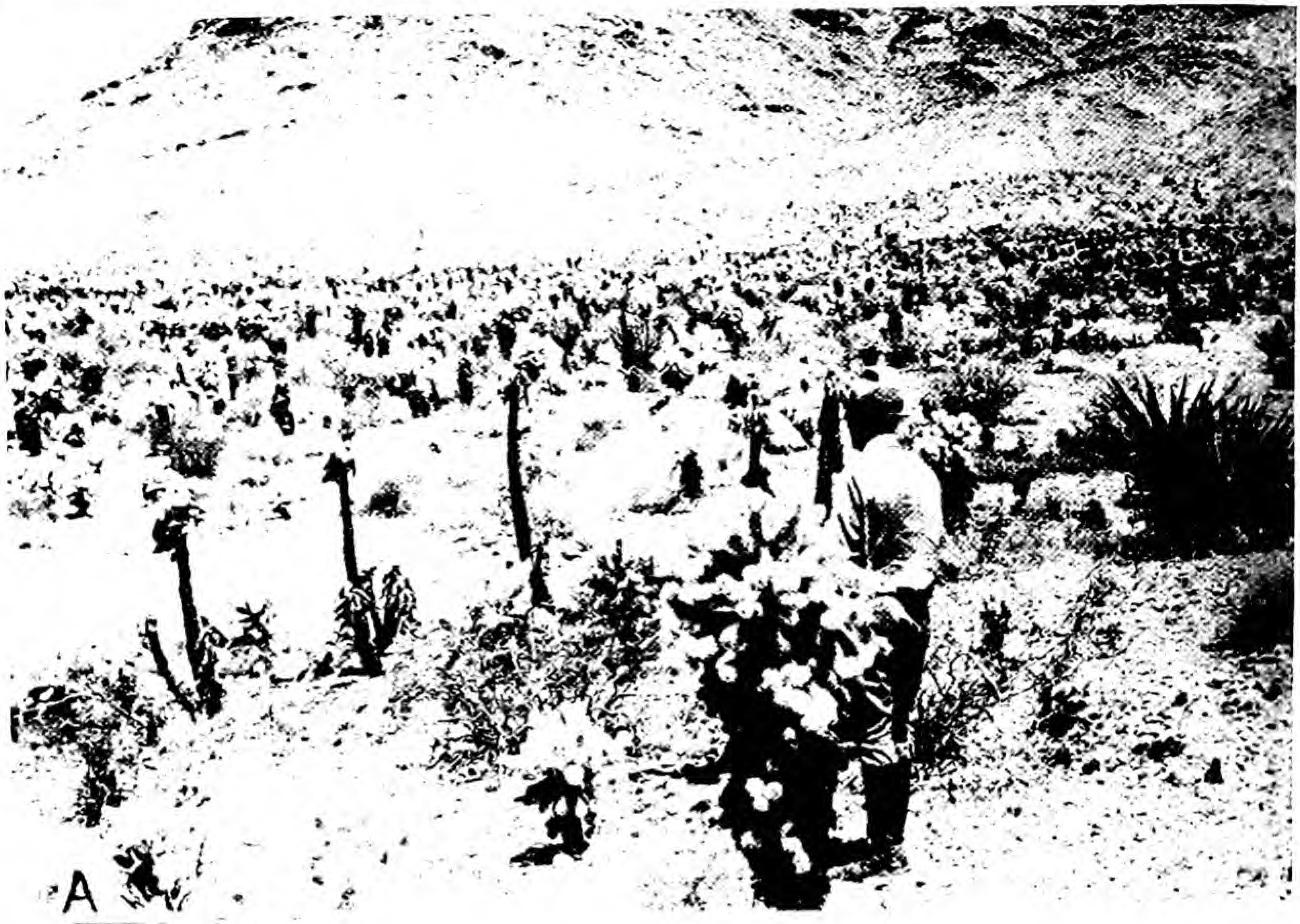
Gutierrezia is also the most important indicator of overgrazing in the eastern portion of the desert plains and in the *Larrea-Flourensia* scrub. In western Mexico and Arizona it is largely or completely replaced by *Isocoma coronopifolia* and its varieties, which are the characteristic indicators from the lowermost *Prosopis* valleys upward into the *Bouteloua-Aristida* grassland. On the *Parkinsonia-Cereus* bajadas and hills, *Franseria deltoidea* is the indicator on lower slopes and *Encelia farinosa*, or more rarely *Chrysoma laricifolia*, on the upper, while *Fran-*



Half-shrubs as indicators of overgrazing.
A. *Yucca glauca*; Colorado Springs, Colorado.
B. *Prosopis* and *Calliandra* in desert plains; Tucson, Arizona.

seria dumosa and, to a less extent, *Hilaria rigida*, play a somewhat similar role in the *Larrea* plains of western Arizona and adjacent California. In the higher desert plains, *Calliandra eriophylla* and *Eriogonum wrighti* largely replace *Isocoma* as the most important indicator, while *Baccharis wrighti* is more local. Other halfshrubs that occur through the desert scrub in varying importance are *Zinnia pumila, Psilostrophe cooperi, Krameria glandulosa, Bebbia juncea*, and *Hymenoclea salsola*. While all of the halfshrubs of the desert scrub and grassland are normally indicators of overgrazing, they follow the rule in that practically every one is grazed to some degree when more palatable forage is lacking. This is altogether exceptional in the case of *Gutierrezia, Isocoma*, and *Franseria*, but all of these were found to be grazed more or less during the severe drouth of 1918 (Plate 34B).

Cacti as Indicators.—Cacti owe their value as indicators of overgrazing to the protection afforded by their spines. Under ordinary conditions this is almost complete protection, but during drouth periods in the Southwest, cattle in particular make much use of cacti and often keep alive upon them as an exclusive diet. At such times they are utilized by jack-rabbits and pack-rats also, and the work of these rodents frequently renders the prickly pears and barrel cacti available for stock. The cacti which serve to indicate overgrazing belong almost wholly to the genus *Opuntia*. The species with flat joints are commonly known as prickly pears, and those with cylindric ones as chollas. In the short grass plains and mixed prairies *Opuntia polyacantha* and *O. mesacantha* are the chief indicators, while *Opuntia arborescens* is often the most important species from the Arkansas Valley southward. Both owe their abundance as much to the great ease of propagation as to their spiny protection. In the case of the chollas especially, the joints are readily broken off and carried about by cattle, and in addition they are blown off by the wind. Moreover, they are well adapted to ecesis in disturbed places, owing to their succulence and the shallow root-system. In the Southwest, the most important cactus indicators in the desert scrub and savanna are *Opuntia fulgida, O. f. mammillata*, and *O. spinosior* among the chollas, and *O. engelmanni, O. discata*, and *O. phaeacantha* among the prickly pears. All these extend up into the grassland to some degree at least, but in the foothills the most common species are *Opuntia versicolor, O. arbuscula, O. bigelovi*, and *O. chlorotica*. *Nolina, Dasylirium*, and *Agave* resemble the cacti more or less in indicator value (Plate 35A).



A. *Opuntia bigelovii* indicator of overgrazing in desert scrub; Mohave Desert.
B. Shrubs as indicators of overgrazing: *Artemisia*, *Ceanothus* and *Quercus*; California.

Shrubs as Indicators.—The shrubs that indicate the overgrazing of grassland are chiefly such dominants of sagebrush, scrub, or chaparral as mix with the grasses to form savanna. The most important are *Artemisia, Prosopus, Acacia, Yucca, Quercus* and *Adenostoma*. They resemble each other in that grazing gives them the advantage in competition with the grasses, partly by decreasing the hold of the latter through eating or trampling, and partly by disseminating the seeds and rendering their germination more certain. This advantage is largely or completely lost in the case of browsing animals, such as goats, since all of them are readily browsed, with the exception of *Yucca* and *Arctostaphylus*. Species of *Artemisia* are the chief shrub indicators of overgrazing in the mixed prairies, short grass plains, and *Agropyrum* bunch grass prairie, though various dominants of the chaparral not infrequently assume this role also. The most widespread and important is *Artemisia tridentata*, while *A. cana* is perhaps the most common in the mixed prairies and *A. filifolia* in sandy areas and sandhills. The lower forms such as *A. trifida*, *A. arbuscula*, *A. rigida*, and *A. spinescens*, might well be regarded as half shrubs. They are more or less widely distributed, but their contact with grassland is more local. In California, fragments of savanna composed of *Artemisia californica* and *Stipa* indicate a similar relation between sagebrush and grassland. This appears to have been true formerly of *Adenostoma* as well, but the observed contacts with *Stipa* grassland are as yet too few for certainty. In the desert plains, *Prosopus*, often with *Acacia* or *Celtis*, is the characteristic shrub indicator of overgrazing. It also extends northward in the short grass plains to southern Colorado and Kansas. It is perhaps the most typical of all such indicators, owing to its height and the ready dissemination of its seeds by cattle. *Quercus virens*, *Q. breviloba*, and *Q. undulata*, as well as other members of the chaparral, take similar parts in the grassland of southwestern Texas and adjacent New Mexico. The role of *Yucca radiosa* and *macrocarpa* as indicators of overgrazing is somewhat less clear, but their constant occurrence in the sandy grasslands of the Southwest and the connection between their propagation and disturbance by cattle seem to leave little doubt of a similar correlation (Plate 35B).

Annuals as Indicators.—Annuals are typically indicators of serious disturbance, and hence serve to mark the existence of harmful overgrazing when abundant. They are the universal pioneers of secondary successions, and they regularly disappear in the course of development.

When the disturbance is continuous or recurrent, they may persist for years, but their seral nature is readily disclosed by protecting an area. In a few cases they become suppressed by the perennials and continue as a dwarfed ground layer. In the Southwest, the winter rains permit a characteristic development of annuals, which complete their growth and mature their seeds before the perennial communities of the summer become controlling. Annuals usually first appear in spots denuded by trampling and extend from these throughout the community in proportion to the degree of overgrazing. Their mobility is often very great and they may take more or less complete control of a badly overgrazed range in a few years. Indications of varying degrees of overgrazing are given by differences in species as well as in density and vigor. The first annuals to appear are native species, or subruderals, which are given a chance to spread or develop because of the trampling and overcropping of the climax dominants. These often give way to more vigorous subruderals, or they become mixed with introduced weeds or ruderals, and are sometimes completely replaced by them. This is usually only when the disturbance has been long continued and the supply of ruderals maintained by the presence of man. In the case of complete replacement, such as by *Avena* or *Bromus*, fire has often played an effective part. When more palatable species have disappeared, annuals often furnish considerable grazing, though it is usually inferior in all respects to that afforded by the climax dominants displaced. *Avena fatua* is an exception to some extent, while in the Southwest the winter annuals are extremely important in tiding over the cattle until the summer grasses appear (Plate 36).

There are several hundred annuals which serve in some degree as overgrazing indicators. The most important ones are found chiefly in the grassland climax and its contacts with the scrub formations. Some of these extend upward into the grasslands of the montane zone, while the indicators of overgrazing in the higher zones usually belong to the same or similar genera. A few of the annual indicators extend more or less throughout the grassland formation, but most of them occur in their particular region. Hence, it seems most convenient to group them under three heads, namely, prairies and plains, desert plains, and bunch grass prairies.

Prairie and Plains Indicators.—While different species of annuals indicate small differences in the degree of overgrazing, the abundance

and height of the plants is usually of greater importance. In addition, annual indicators have received little quantitative study, and hence it is possible only to list them in the general order of their importance. Some of those listed are either annual or biennial, and a few are typically biennial.

Plantago patagonica	Eriogonum cernuum	Polygonum ramosissimum
Festuca octoflora	Eragrostis pilosa	Aster tancetifolius
Hedeoma hispida	Eragrostis major	Aster canescens
Lepidium intermedium	Ambrosia artemisifolia	Phacelia heterophylla
Lepidium alyssoides	Salsola kali	Allionia linearis
Lepidium ramosum	Solanum rostratum	Cassia chamaecrista
Lappula texana	Argemone platyceras	Coreopsis tinctoria
Verbena bracteosa	Dysodia papposa	Salvia lanceolata
Helianthus petiolaris	Hordeum jubatum	Lupinus pusillus
Helianthus annuus	Schedonnardus texanus	Lotus americanus
Erigeron canadensis	Munroa squarrosa	Draba caroliniana
Erigeron divergens	Euphorbia marginata	Myosurus minimus
Erigeron ramosus	Croton texensis	Androsace occidentalis
Chenopodium leptophyllum	Collomia linearis	Pectis angustifolia
Chenopodium album	Verbesina encelioides	Sophia pinnata
Eriogonum annuum	Orthocarpus luteus	Physalis lobata
	Polygonum aviculare	Solanum triflorum

Desert Plains Indicators.—These fall into two groups, depending upon their time of appearance. The summer annuals correspond to those listed above. They occur with the grasses, and hence are a more exact measure of overgrazing than the winter annuals. Most of them are distributed throughout the region, but are more typical in New Mexico. The winter annuals develop most abundantly in overgrazed areas also, but they finish their growth before the grasses appear and hence indicate conditions of the previous year. They are characteristic of southern Arizona and adjacent Mexico. The most important ones, such as *Plantago fastigiata, Eschscholtzia mexicana, Lesquerella gordoni, Lepidium lasiocarpum, Pectocarya linearis*, etc. often form a dense cover and are invaluable for spring grazing.

Summer Annuals

Aristida bromoides	Kallstroemia brachystylis	Haplopappus gracilis
Bouteloua aristoides	Kallstroemia hirsutissima	Eriogonum albertianum
Bouteloua polystachya	Calothrix lanuginosa	Eriogonum polycladum
Boerhavia torreyana	Croton corymbulosus	Pectis angustifolia
Boerhavia intermedia	Solanum elaeagnifolium	Pectis prostrata
Kallstroemia grandiflora	Tribulus terrestris	Chloris elegans
Kallstroemia parviflora	Portulaca oleracea	Eragrostis pilosa

Winter Annuals

Plantago fastigiata	Erodium cicutarium	Malacothrix sonchoides
Eschscholtzia mexicana	Erodium texanum	Malacothrix fendleri
Lesquerella gordoni	Phacelia distans	Oenothera primaveris
Lepidium lasiocarpum	Phacelia crenulata	Calandrinia menziesi
Pterocarya linearis	Lupinus sparsiflorus	Baeria gracilis
Bowlesia lobata	Thelypodium lasiophyllum	Lappula texana
Plagiobothrys arizonicus	Thysanocarpus curvipes	Festuca octoflora
Amsinckia tessellata	Lotus humistratus	Gilia gracilis
Sophia pinnata		Salvia columbariae
Daucus pusillus		

Bunch Grass Prairie Indicators.—The most remarkable development of annual indicators of overgrazing has taken place in California. This is undoubtedly a consequence of its early settlement, together with its mild climate and winter rainfall. In addition to a large number of summer and winter annuals derived from the native vegetation, the most widespread and typical indicators are European weeds, which are nearly all grasses. Many of these were probably introduced from Europe during the period of Spanish occupation, and spread rapidly as a result of overgrazing and fire. These agencies would have first brought about the replacement of the native *Stipas,* but sooner or later fire and clearing would have caused weeds to spread through much of the chaparral as well. This problem of successive invasions and replacements is now under investigation by means of permanent protected quadrats. Meanwhile, the conclusions reached by Davy (1902) afford the best summary of the probable course of development:

"1. The primitive forage plants were the 'bunch grasses,' (*Danthonias, Stipas, Melicas, Poas,* and perennial *Festucas*), with annual and perennial clovers, wild-pea vines and wild sunflowers; these were much more abundant in former times than now, and on account of their palatableness they largely disappeared with overstocking.

"2. With the advent of white settlers and their domestic animals, wild oats (*Avena fatua*) and alfilerilla (*Erodium cicutarium*) took possession of the country; these increased in relative abundance as the native forage plants became scarce; as the latter diminished in quantity, the cattle took to eating the former until they in like manner succumbed, while other plants took their place.

"3. Small barley grass (*Hordeum maritimum gussoneanum*) squirrel-tail (*Festuca myurus*), and soft chess (*Bromus hordeaceus*) were

among the next weedy introductions; the two former, when in a maturing condition being disliked by cattle, have had a chance to spread and cover the ranges; but cattle having acquired a taste for soft chess, it is being kept in check, if not diminishing, on closely grazed ranges.

"4. A third immigration is now taking place, in which musky alfilerilla (*Erodium moschatum*), broncho grass (*Bromus maximus gussoni*), barley grass (*Hordeum murinum*, locally called fox-tail), tacalote (*Centaurea melitensis*), hawkbit (*Hypochaeris glabra*), bur-clover (*Medicago denticulata*), and other weeds are establishing themselves along the roadside and around ranch houses. Of these, the bur-clover and musky alfilerilla have some forage value. Barley grass is eaten green in the spring before heading out, but afterwards becomes one of the most objectionable weeds for a stock range. The other aliens are destined to cause irreparable injury to the ranges unless kept in check and prevented from becoming firmly established."

With few exceptions the species listed below are summer annuals. The winter annuals of southern California are largely those noted for the desert plains, but they are here relatively unimportant. It should be borne in mind that, while the indicators given, originally denoted overgrazing, some of them such as *Avena* and *Erodium*, have become valuable forage plants as a consequence of the displacement of the native bunch grasses, and in turn their overgrazed condition is indicated by still more weedy invaders.

Grass Indicators

Avena fatua
Bromus maximus
Bromus rubens
Bromus hordeaceus
Bromus tectorum
Festuca myurus
Hordeum maritimum gussoneanum
Hordeum murinum
Polypogon monspeliensis
Lamarckia aurea

Forb Indicators

Erodium cicutarium
Erodium moschatum
Centaurea melitensis
Medicago denticulata
Hypochaeris glabra
Hypochaeris radicata
Eriogonum vimineum
Eriogonum nudum
Lupinus micranthus
Lupinus affinis
Lupinus truncatus
Trifolium microcephalum
Trifolium amplectens
Trifolium gracilentum
Trifolium tridentatum
Medicago lupulina
Melilotus indica
Raphanus raphanistrum
Eryngium vaseyi
Hemizonia fitchi
Hemizonia clevelandi
Madia exigua
Madia dissitiflora
Lotus strigosus

Trichostema lanceolatum	Lagophylla ramosissima	Eremocarpus setigerus
Plantago patagonica	Ptilonella scabra	Lithospermum ruderale
Epilobium paniculatum	Orthocarpus purpurascens	Navarretia leucophaea
Phacelia heterophylla	Centaurea cyanus	

Great Basin Indicators.—These are limited in the present discussion to the annuals that spread over the grassy intervals of the sagebrush, especially along the northern border where it is mixed with *Agropyrum spicatum*. While a number of the annuals of the preceding list assume this role along the western edge, three species of introduced weeds are more important than all others combined; these are *Bromus tectorum, Sisymbrium altissimum*, and *Lepidium perfoliatum* which occur singly or variously mixed. The most extensive community is that of *Bromus tectorum*, while the mixed community of *Bromus* and *Sisymbrium* is almost equally important. *Lepidium* is most abundant in the Northwest, but is rapidly spreading to other regions. While they owe their establishment originally to overgrazing, fire is a large factor in their rapid spread. They have now replaced the native grasses and herbage almost completely over thousands of square miles, and have reduced the grazing value practically to that of sagebrush alone. *Bromus* is the only one with any real value, and this is frequently slight. It furnishes some grazing for sheep in the spring, but quickly becomes dry and nearly worthless (Plate 36).

Overgrazing in the Past.—The condition of the great ranges of the prairies and plains before the settlement of the West and the effect of settlement upon the grasses have long been mooted questions. It has frequently been assumed that certain grasses have disappeared with the coming of the early settlers and that others have entered to take their place. For example, it has been the almost universal opinion of farmers and stockmen that buffalo grass vanished from the prairies with the going of the buffalo and that the bluestems had come in from the East to replace it. This opinion has been shared to a large degree by scientific men. Bessey (1887) early noted the general relations of the grasses to cultivation and fire:

"Several entirely distinct species are popularly known as buffalo grass. All, however, are short grasses, unfit for making into hay, and although apparently quite nutritious, they supply so small an amount of food per acre that as the land becomes more valuable the farmer cannot afford to retain them. But even should he wish to retain them, he can not; for they are unfitted to battle successfully with bluegrass and

A. *Bromus tectorum* indicating fire as well as overgrazing, in Great Basin sagebrush, Boise, Idaho.

B. *Erodium cicutarium* indicating trampling as well as [illegible] grassland, Oracle, [illegible].

white clover, with the bluestems and rank weeks which always spring into prominence upon the prairies when the settler stops the annual prairie fires. Moreover, they cannot endure the close cropping and trampling to which they are subjected when the land is enclosed and used for regular farming purposes. Already the genuine buffalo grass (*Buchloe dactyloides*) has practically disappeared from the eastern third of the State. Of course I know very well that there are patches of it here and there in these older counties; it may be found in such patches within a mile or two of the capitol building; but these little patches are as nothing when compared with its former extensive distribution. A second grass commonly known by the name of buffalo grass (*Bouteloua gracilis*: blue grama) is fast following the first."

Chapter IV

NATURE AND STRUCTURE OF THE CLIMAX

The Climax Concept

More than a century ago when Lewis and Clark set out upon their memorable journey across the continent of North America (1803-6), they were the first to traverse the great climaxes from deciduous woods in the East through the vast expanse of prairie and plain to the majestic coniferous forest of the Northwest. At this time the oak-hickory woodland beyond the Appalachians was almost untouched by the ax except in the neighborhood of a few straggling pioneer settlements, and west of the Mississippi hardly an acre of prairie had known the plow. A few years later (1809), Bradbury states that "the boundless prairies are covered with the finest verdure imaginable and will become one of the most beautiful countries in the world, while the plains are of such extent and fertility as to maintain an immense number of animals." It appears probable that at this time no other grassland in the world exhibited such myriads of large mammals belonging to but a few species.

The natural inference has been that the prairies were much modified by the grazing of animals and the fires of primitive man, and this has been reinforced by estimates of the population of each. Seton concludes that the original number of bison was about 60 million with a probable reduction to 40 million by 1800, and that both the antelope and white-tailed deer were equally abundant, while elk and mule-deer amounted to not more than 10 million at the maximum. However, these were distributed over a billion or two acres, and the average density was probably never more than a score to the square mile.

Estimates of the Indian tribes show the greatest divergence, but it seems improbable that the total population within the grassland ever exceeded a half million. The general habit of migration among the animals further insured that serious effects from overgrazing and trampling were but local or transitory, while the influence of fires set by the Indians was even less significant in modifying the plant cover. As to the forests, those of the Northwest were still primeval and in the East they were yet to be changed over wide areas by lumbering and burning on a large scale.

The idea of a climax in the development of vegetation was first

suggested by Hult in 1885 and then was advanced more or less independently by several investigators during the next decade or so (1916; 1935). It was applied to a more or less permanent and final stage of a particular succession and hence one characteristic of a restricted area. The concept of the climax as a complex organism inseparably connected with its climate and often continental in extent was introduced by Clements in 1916. According to this view, the climax constitutes the major unit of vegetation and as such forms the basis for the natural classification of plant communities. The relation between climate and climax is considered to be the paramount one, while the intimate bond between the two is emphasized by the derivation of the terms from the same Greek root. In consequence, under this concept climax is invariably employed with reference to the climatic community alone, namely, the formation or its major divisions.

At the outset it was recognized that animals must also be considered members of the climax, and the word biome was proposed for the purpose of laying stress upon the mutual roles of plants and animals.

With this went the realization that the primary relations to the habitat or ece were necessarily different by virtue of the fact that plants are producents and animals consuments. On land, moreover, plants constitute the fixed matrix of the biome in direct connection with the climate, while the animals bear a dual relation, to plants as well as to climate. The outstanding effect of the one is displayed in reaction upon the ece, of the other in coaction upon plants, which constitutes the primary bond of the biotic community.

Because of its emphasis upon the climatic relation, the term climax has come more and more to replace the word formation, which is regarded as an exact synonym, and this process may have been favored by a tendency to avoid confusion with the geological use. The designation "climatic formation" has now and then been used, but this is merely to accentuate its nature and to distinguish it from less definite usages. Furthermore, climax and biome are complete synonyms when the biotic community is to be indicated, though climax will necessarily continue to be employed for the matrix when plants alone are considered.

Nature of the Climax

This theme has been developed in considerable detail in earlier works (1916, 1920, 1928, 1929), as well as in a comprehensive treatment by

Phillips (1935), and hence a summary account of the major features will suffice in the present place. These may be conveniently grouped under the following four captions, i.e., unity, stabilization and change, origin and relationship, and objective tests.

Unity of the Climax.—The inherent unity of the climax rests upon the fact that it is not merely the response to a particular climate, but is at the same time the expression and the indicator of it. Because of extent, variation in space and time, and the usually gradual transition into adjacent climates, to say nothing of the human equation, neither physical nor human measures of a climate are adequately satisfactory. By contrast, the visibility, continuity, and sessile nature of the plant community are peculiarly helpful in indicating the fluctuating limits of a climate, while its direct response in terms of food-making, growth and life-form provides the fullest possible integration of physical factors. Naturally, both physical and human values have a part in analyzing and in interpreting the climate as outlined by the climax, but these can only supplement and not replace the biotic indicators.

It may seem logical to infer that the unity of both climax and climate should be matched by a similar uniformity, but reflection will make clear that such is not the case. This is due in the first place to the gradual but marked shift in rainfall or temperature from one boundary to the other, probably best illustrated by the climate of the prairie. In terms of precipitation, the latter may range along the parallel of 40° from nearly 40 in. at the eastern edge of the true prairie to approximately 10 in. at the western border of the mixed grassland, or even to 6 in. in the desert plains and the Great Valley of California. Such a change is roughly 1 in. for 50 miles and is regionally all but imperceptible. The temperature change along the 100th meridian from the mixed prairie in Texas to that of Manitoba and Saskatchewan is even more striking, since only one association is concerned. In southern Texas the average period without killing frost is about 9 months but in the Canadian provinces it is less than 3, while the mean annual temperatures are 70 and 33° F. respectively. The variation of the two major factors at the extremes of the climatic cycle is likewise great, the maximum rainfall not infrequently amounting to three or four times that of the minimum.

The visible unity of the climax is due primarily to the life-form of the dominants, which is the concrete expression of the climate. In prairie and steppe, this is the grass form, with which must be reckoned the

sedges, especially in the tundra. The shrub characterizes the two scrub climaxes of North America, namely, desert, and chaparral, while the tree appears in three subforms, coniferous, deciduous, and broad-leaved evergreen, to typify the corresponding boreal, temperate, and tropical climaxes. The life-form is naturally reflected in the genus, though not without exceptions, since two or more forms or subforms, herb or shrub, deciduous or evergreen, annual or perennial, may occur in the same genus. Hence, the essential unity of a climax is to be sought in its dominant species, since these embody not only the life-form and the genus, but also denote in themselves a definite relation to the climate. Their reactions and coactions are the most controlling both in kind and amount, and thus they determine the conditions under which all the remaining species are associated with them. This is true to a less degree of the animal influents, though their coactions may often be more significant than those of plants.

Stabilization and Change.—Under the growing tendency to abandon static concepts, it is comprehensible that the pendulum should swing too far and change be overstressed. This consequence is fostered by the fact that most ecological studies are carried out in settled regions where disturbance is the ruling process. As a result, the climax is badly fragmented or even absent over wide areas and subseres are legion. In all such instances it is exceedingly difficult or entirely impossible to strike a balance between stability and change, and it becomes imperative to turn to regions much less disturbed by man, where climatic control is still paramount.

It is likewise essential to employ a conceivable measure of time, such as can be expressed in human terms of millennia rather than in eons. No student of past vegetation entertains a doubt that climaxes have evolved, migrated and disappeared under the compulsion of great climatic changes from the Paleozoic onward, but he is also insistent that they persist through millions of years in the absence of such changes and of destructive disturbances by man. There is good and even conclusive evidence within the limitations of fossil materials that the prairie climax has been in existence for several millions of years at least and with most of the dominant species of today. This is even more certainly true of forests on the Pacific Coast, owing to the wealth of fossil evidence, while the generic dominants of the deciduous forests of the Dakota Cretaceous and of today are strikingly similar.

It can still be confidently affirmed that stabilization is the universal tendency of all vegetation under the ruling climate, and that climaxes are characterized by a high degree of stability when reckoned in thousands or even millions of years. No one realizes more clearly than the devotee of succession that change is constantly and universally at work, but in the absence of civilized man this is within the fabric of the climax and not destructive of it. Even in a country as intensively developed as the Middle West, the prairie relicts exhibit almost complete stability of dominants and subdominants in spite of being surrounded by cultivation. It is obvious that climaxes display superficial changes with the season, year or cycle, as in aspection and annuation, but these modify the matrix itself little or not at all. The annuals of the desert may be present in millions one year and absent the next, or one dominant grass may seem prevailing one season and a different one the following year, but these changes are merely recurrent or indeed only apparent. While the modifications represented by bare areas and by seres in every stage are more striking, these are all in the irresistible process of being stabilized as rapidly as the controlling climate and the interference of man permit.

In brief, the changes dues to aspection, annuation or natural coaction are superficial, fleeting or periodic and leave no permanent impress, while those of succession are an intrinsic part of the stabilizing process. Man alone can destroy the stability of the climax during the long period of control by its climate, and he accomplishes this by fragments in consequence of a destruction that is selective, partial or complete, and continually renewed.

Origin and Relationship.—Like other but simpler organisms, each climax not only has its own growth and development in terms of primary and secondary succession, but it has also evolved out of a preceding climax. In other words, it possesses an ontogeny and phylogeny that can be quantitatively and experimentally studied, much as with the individuals and species of plants and animals. Out of the one has come widespread activity in the investigation of succession, while interest in the other lingers on the threshold, chiefly because it demands a knowledge of the climaxes of more than one continent. With increasing research in these, especially in Europe and Asia, it will be possible to test critically the panclimaxes already suggested, as well as to determine the origin and relationships of the constituent formations (1916, 1929).

This task will also require the services of paleo-ecology for the recon-

struction of each eoclimax, which has been differentiated by worldwide climatic changes into the existing units of the panclimax or panformation. As it is, there can be no serious question of the existence of a great hemispheric clisere constituted by the arctic, boreal, deciduous, grassland, subtropical and tropical panclimaxes. Desert formations for the most part constitute an exception and may well be regarded as endemic climaxes evolved in response to regional changes of climate (1936).

It is a significant fact that the boreal formations of North America and Eurasia are more closely related than the coniferous ones of the former, but this seeming anomaly is explained by the greater climatic differences that have produced the forests of the Petran and Sierran systems. The five climaxes concerned are relatively well known, and it is possible to indicate their relationships with some assurance, and all the more because of their parallel development on the two great mountain chains. In the case of deciduous forest and grassland, only a single formation of each is present in North America, and the problem of differentiation resolves itself into tracing the origin and relationship of the several associations. It has been suggested that the mixed prairie by virtue of its position, extent and common dominants represents the original formation in Tertiary times, an assumption reinforced by its close resemblance to the steppe climax. It is not improbable that the mixed hardwoods of the southern Appalachians bear a similar relation to the associations of the modern deciduous forest.

Tests of a Climax.—As has been previously indicated, the major climaxes of North America, such as tundra, boreal and deciduous forest, and prairie, stand forth clearly as distinct units, in spite of the fact that the prairie was first regarded as comprising two formations, as a consequence of the changes produced by overgrazing. The other coniferous and the scrub climaxes emerge less distinctly because of the greater similarity of life-form within each group, and hence it is necessary to appeal to criteria derived from the major formations just mentioned. This insures uniformity of basis and a high degree of objectivity, both of which are qualities of paramount importance for the natural classification of biomes. In fact, entire consistency in the application of criteria is the best warrant of objective results, though this is obviously a procedure that demands a firsthand acquaintance with most if not all the units concerned and over a large portion of their respective areas.

The primary criterion is that afforded by the vegetation-form, as is.

illustrated by the four major climaxes. The others of each group, such as coniferous forest or scrub, are characterized also by the same form in the dominants, but this is not decisive as between related climaxes and hence recourse must be taken to the other tests. The value of the life-form is most evident where two climaxes of different physiognomy are in contact, as in the case of the lake forest of pine-hemlock and the deciduous forest of hardwoods. The static view would make the hemlock in particular a dominant of the deciduous formation, but the evidence derived from the vegetation-form is supported by that of phylogeny and by early records of composition and timber-cut to show that two different climaxes are concerned. Secondary forms or subforms rarely if ever mark distinctions between climaxes, but do aid in the recognition of associations. This is well exemplified by the tall, mid and short grasses of the prairie and somewhat less definitely by the generally deciduous character of the Petran chaparral and the typically evergreen nature of the Sierran.

As would be expected, the most significant test of the unity of a formation is afforded by the presence of certain dominant species through all or nearly all of the associations, but often not in the role of dominants by reason of reduced abundance. Here again perhaps the best examples are furnished by prairie and tundra, though the rule applies almost equally well to deciduous forest and only less so to coniferous ones because of a usually smaller number of dominants. For the prairie, the number of such species, or predominants, found in all or all but one or two of the five associations is eight, namely, *Stipa comata, Agropyrum smithi, Bouteloua gracilis, Sporobolus cryptandrus, Koeleria cristata, Elymus sitanion, Poa scabrella* and *Festuca ovina*. Even when a species is lacking over most of an association, as in the case of *Stipa comata* and the true prairie, it may be represented by a close relative, such as *S. spartea*, which is probably no more than a mesic variety of it. As to the three associations of the deciduous forest, a still larger number of dominant species occur to some degree in all; the oaks comprise *Quercus borealis, velutina, alba, macrocarpa, coccinea, muhlenbergi, stellata* and *marilandica*, and the hickories, *Carya ovata, glabra, alba* and *cordiformis*.

It was the application of this test by specific dominants that led to the recognition of the two climaxes in the coniferous mantle of the Petran and Sierran cordilleras. The natural assumption was that such a

narrow belt could not contain more than one climax, especially in view of its physiognomic uniformity, but this failed to reckon with the great climatic differences of the two portions and the corresponding response of the dominants. The effect of altitude proved to be much more decisive than that of region, dominants common to the montane and subalpine zones being practically absent, though the rule for the same zone in each of the two separate mountain systems. Long after the presence of two climaxes had been established, it was found that Sargent had anticipated this conclusion, though in other terms.

As would be inferred, the dominants of related associations belong to a few common genera for the most part. Thus, there are a dozen species of *Stipa* variously distributed as dominants through the grassland, nearly as many of *Sporobolus, Bouteloua* and *Aristida,* and several each of *Poa, Agropyrum, Elymus, Andropogon, Festuca* and *Muhlenbergia.* In the deciduous forest, *Quercus, Carya* and *Acer* are the great genera, and for the various coniferous ones, *Pinus, Abies* and *Picea,* with species of *Tsuga, Thuja, Larix* and *Juniperus* hardly less numerous.

The perennial forbs that play the part of subdominants also possess considerable value in linking associations together, and to a higher degree in the deciduous forest than in the prairie, owing chiefly to the factors of shade and protection. Over a hundred subdominants belonging to two score or more of genera, such as *Erythronium, Dicentra, Trillium, Aquilegia, Arisaema, Phlox, Uvularia, Viola, Impatiens, Desmodium, Helianthus, Aster* and *Solidago,* range from Nova Scotia or New England beyond the borders of the actual climax to Nebraska and Kansas. Across the wide expanse of the prairie climax, species in common are only exceptional, these few belonging mostly to the composites, notably *Grindelia squarrosa, Gutierrezia sarothrae, Artemisia dracunculus* and *vulgaris.* On the other hand, the number of genera of subdominants found throughout the grassland is very large.

The greater mobility of the larger mammals in particular renders animal influents less significant than plants as a criterion, but several of these possess definite value and the less mobile rodents even more. The antelope and bison are typical of the grassland climax, the first being practically restricted to it, while jack-rabbits, ground-squirrels and kangaroo-rats are characteristic dwellers in the prairie, as is their chief foe, the coyote.

The remaining criteria are derived from development directly or

indirectly, though this is less evident in the case of the ecotone between two associations. Here the mixing of dominants and subdominants indicates their general similarity in terms of the formation, within which range their preferences assign them to different associations. The evidence from primary succession is of value only in the later stages as a rule, since initial associes like the reed-swamp may occur in several climaxes. With subseres, however, all or nearly all the stages are related to the particular climax and such seres denote a corresponding unity in development. This is especially true of all subclimaxes and most evidently in the case of those due to fire. More significant still are postclimaxes in both grassland and forest. For example, the associes of species of *Andropogon,* which is subclimax to the oak-hickory forest, constitutes a postclimax to five out of the six associations of the prairie. On the other hand, the community of *Ulmus, Juglans, Fraxinus,* etc., found on the flood-plains through the region of deciduous forest, forms a common subclimax to the three associations.

In addition to such ontogenetic criteria, phylogeny supplies tests of even greater value. This is notably the case with the two associations of the montane and subalpine coniferous forests of the West, though perhaps the most striking application of this criterion is in connection with the lake forest of pine-hemlock. The concrete evidence for such a climax recurs constantly through the region of the Great Lakes to the Atlantic but it is fragmentary and there is no evident related association to the westward. However, the four genera are represented by related species in the two regions, namely, *Pinus strobus* by *P. monticola, P. banksiana* by *P. contorta, Tsuga canadensis* by *T. heterophylla, Larix laricina* by *L. occidentalis,* and *Thuja occidentalis* by *T. plicata,* although the last two genera have changed from a subclimax role in the East to a climax one in the West. As suggested earlier, phylogenetic evidence of still more direct nature is supplied by the mixed prairie with the other enclosing associations and by the remnants of a virgin deciduous forest that exhibits a similar genetic and spatial relation to the associations of this climax.

Finally, it is clear that any test will gain in definiteness and accuracy of application whenever dependable records are available with respect to earlier composition and structure. These may belong entirely to the historical period, as in the case of scientific reports or land surveys, they may bridge the gap between the present and the past as with pollen statistics, or they may reach further back into the geological record, as with

leaf-impressions or other fossils. Two instances of the scientific record that are of the first importance may be given as examples. The first is the essential recognition in 1884 by Sargent of the pine-hemlock climax under the name of the northern pine belt, at a time when relatively little of this had been logged, by contrast with 90 percent or more at present. The second is an account, discovered and communicated by Dr. Vestal, of the prairies of Illinois as seen by Short about 1840. This is of heightened interest since its discovery followed little more than a year after repeated field trips had led to the conclusion that all of Iowa, northern Missouri and most of Illinois were to be assigned to the true prairie, a decision confirmed for Illinois by Short's description, and supported by the more general accounts of Bradbury about 1815, and Greeley in 1860. The true prairie is characterized by three eudominants, *Stipa spartea, Sporobolus asper* and *S. heterolepis*. The presence of tall grasses in it to-day, particularly *Andropogon furcatus* and nutans, is the mark of the disclimax due to the varied disturbances associated with settlement.

Climax and Proclimax

Essential Relations.—In accordance with the view that development regularly terminates in the community capable of maintaining itself under a particular climate, except when disturbance enters, there is but one kind of climax, namely that controlled by climate. This essential relation is regarded as not only inherent in all natural vegetation, but also as implicit in the cognate nature of the two terms. While it is fully recognized that succession may be halted in practically any stage, such communities are invariably subordinate to the true climax as determined by climate alone. From the very meaning of the word, there cannot be climaxes scattered along the developmental route with a genuine climax at the end. There is no intention to question the reality of such pauses, but only to emphasize the fact that they are of a different order from the climax.

While it is natural to express new ideas by qualifying an old term, this does not conduce to the clearest thinking or the most accurate usage. Even more undesirable is the fact that the meaning of the original word is gradually shifted until it becomes either quite vague or hopelessly inclusive. At the hands of some, climax has already suffered this fate, and fire, disease, insects, and human disturbances of all sorts are assumed to

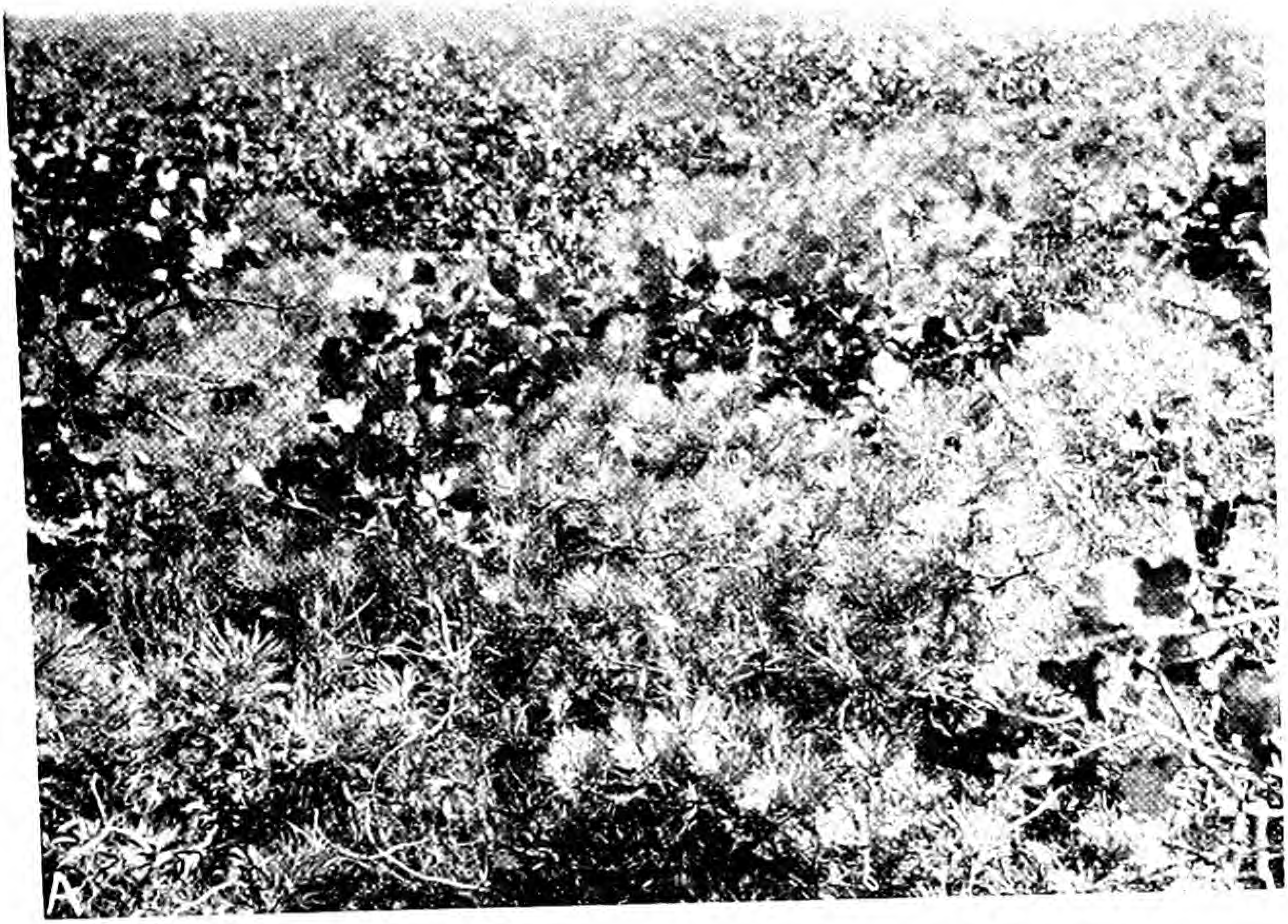
A. Sierran subalpine climax: consociation of *Tsuga mertensiana*, Crater Lake, Oregon.
B. Proclimax of sagebrush (*Artemisia tridentata*), a disclimax due to overgrazing of mixed prairie; climatically a preclimax.

produce corresponding climaxes. On such an assumption corn would constitute one climax, wheat another, and cotton a third, and it would then become imperative to begin anew the task of properly analyzing and classifying vegetation.

In the light of two decades of continued analysis of the vegetation of North America, as well as the application of the twin concepts of climax and complex organism by workers in other portions of the globe and the strong support brought to them by the rise of emergent evolution and holism (1935), the characterization of the climax as given in *Plant Succession* in 1916, still appears to be both complete and accurate. "The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures and dies. Its response to the habitat is shown in processes or functions and in structures that are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, of which all initial and medial stages are but stages of development. . . . A formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession that terminates in the highest life-form possible in the climate concerned." (Plate 37A).

To-day this statement would need modification only to the extent of substituting "biome" for climax or formation and "biotic" for vegetational. This characterization has been annotated and confirmed by Phillips' masterly discussion of climax and complex organism, a treatise that should be read and digested by everyone interested in the field of dynamic ecology and its wide applications.

Proclimaxes. (Plate 37B).—As a general term, proclimax includes all the communities that simulate the climax to some extent in terms of stability or permanence but lack the proper sanction of the existing climate. Certain communities of this type were called potential climaxes in *Plant Succession*, and two kinds were distinguished, namely, preclimax and postclimax. To avoid proposing a new term in advance of its need, subclimax was made to do double duty, denoting both the subfinal stage of succession, as well as apparent climaxes of other kinds. This dual usage was criticized by Godwin, and partially justified by Tansley in an



A. Fire subclimax of dwarf *Pinus* and *Quercus*, the "Plains," New Jersey Pine-barrens.
B. Subclimax of consocies of *Aristida purpurea* in field abandoned 15 years, Great Plains.

appended note on the ground just given. However, this discussion made it evident that a new term was desirable and proclimax was accordingly suggested. While this takes care of the use of subclimax in the second sense noted above, it is better adapted by reason of its significance to apply to all kinds of subpermanent communities other than the climax proper. However, there is still an important residuum after subclimax, preclimax and postclimax have been recognized, and it is proposed to call these *disclimaxes*, as indicated later.

The proclimax may be defined as any more or less permanent community resembling the climax in one or more respects, but gradually replaceable by the latter when the control of climate is not inhibited by disturbance. Besides its general function, it may be used as a synonym for any one of its divisions, as well as in cases of doubt pending further investigation, such as in water climaxes. The four types to be considered are subclimax, disclimax, preclimax and postclimax.

Subclimax (Plate 38).—As the stage preceding the climax in all complete seres, primary and secondary, the subclimax is as universal as it is generally well understood. The great majority of such communities belong to the subsere, especially that following fire, owing to the fact that disturbance is to-day a practically constant feature of most climaxes. Fire and fallow are recurrent processes in cultivated regions generally and they serve to maintain the corresponding subsere until protection or conversion terminates the disturbance. Though the subclimax is just as regular a feature of priseres, these have long ago ended in the climax over most of the climatic area and the related subclimax communities are consequently much restricted in size and widely scattered. Smallness is naturally a characteristic of nearly all subclimaxes, the chief exceptions being due to fire or to fire and logging combined, but by contrast they are often exceedingly numerous.

Because of its position in the succession, the subclimax resembles the preclimax in some respects and in a few instances either term may be properly applied. The distinction between subclimax and disclimax presents some difficulty now and then, as the amount of change necessary to produce the latter may be a matter of judgment. This arises in part also from the structural diversity of formation and association, as a consequence of which the dominants of a particular type of subsere vary in different areas. When there is but a single dominant, as in many burn subclimaxes, no question ensues, but if two or more are present, the deci-

sion between subclimax and disclimax may be less simple, as is not infrequent in scrub and grassland.

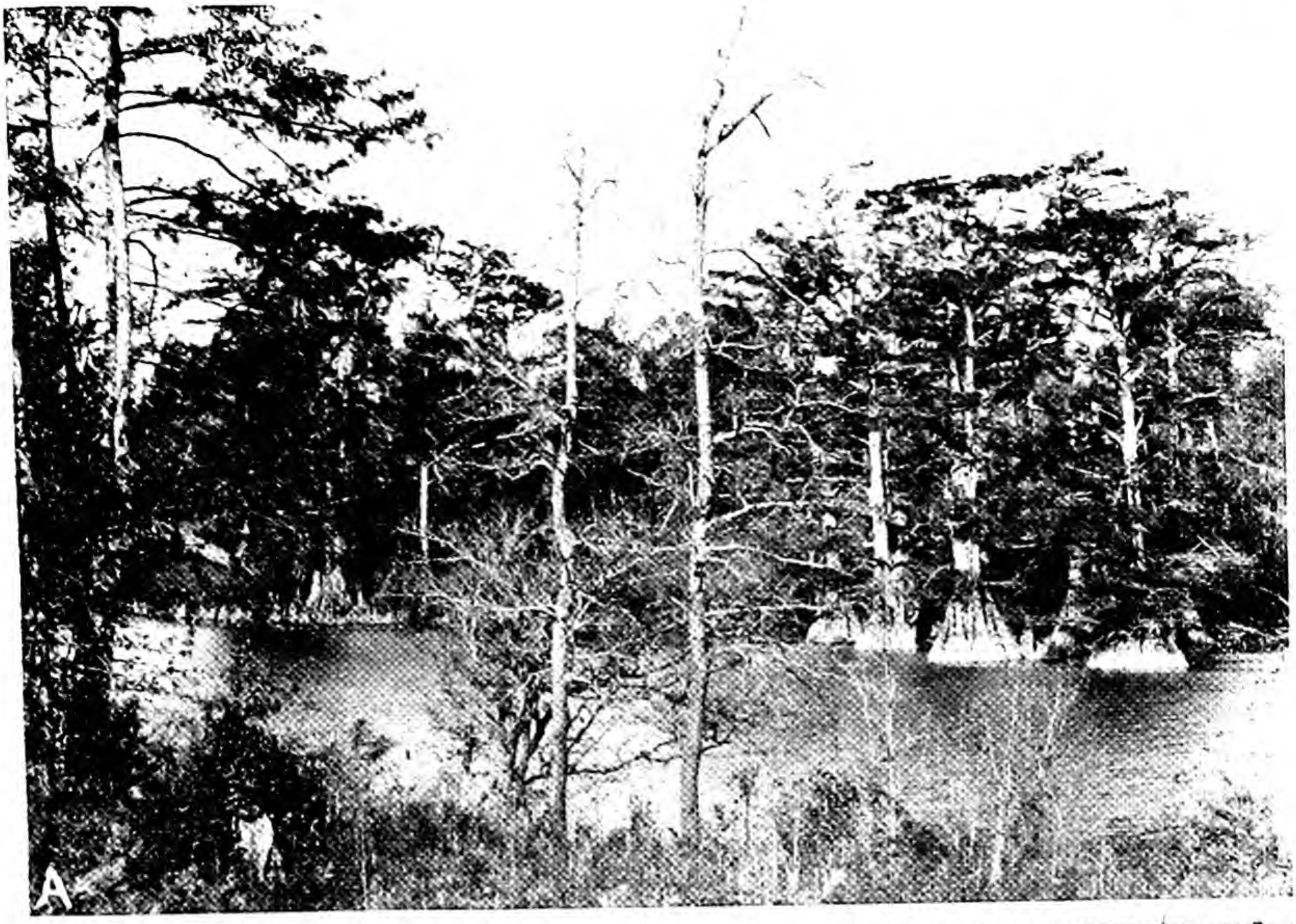
Examples of the subclimax are legion, the outstanding cases being mostly due to fire, alone or after lumbering or clearing. Most typical are those composed of "jack-pines" or species with closed cones that open most readily after fire. Each great region has at least one of these, e.g. *Pinus rigida, virginiana* and *echinata* in the East, *P. banksiana* in the North, *P. murrayana* in the Rocky Mountains, and *P. tuberculata, muricata* and *radiata* on the Pacific Slope. *Pinus palustris* and *P. taeda* play a similar role in the "piney" woods of the Atlantic Gulf region, as does *Pseudotsuga taxifolia* in the Northwest. The characteristic subclimaxes of the boreal forest are composed of aspen (*Populus tremuloides*), balsam-poplar (*P. balsamifera*), and paper-birch (*Betula papyrifera*), either singly or in various combinations. Aspen also forms a notable subclimax in the Rocky Mountains, for the most part in the subalpine zone. Prisere subclimaxes are regular features of bogs and muskeags throughout much or all of the boreal and lake forests, the three dominants being *Larix laricina, Picea mariana* and *Thuja occidentalis*, often associated as zonal consocies. Where pines are absent in the region of the deciduous forest, two xeric oaks, *Quercus stellata* and *marilandica*, may constitute a subclimax, and this role is sometimes assumed by small trees, *Sassafras*, *Diospyrus* and *Hamamelis* being especially important.

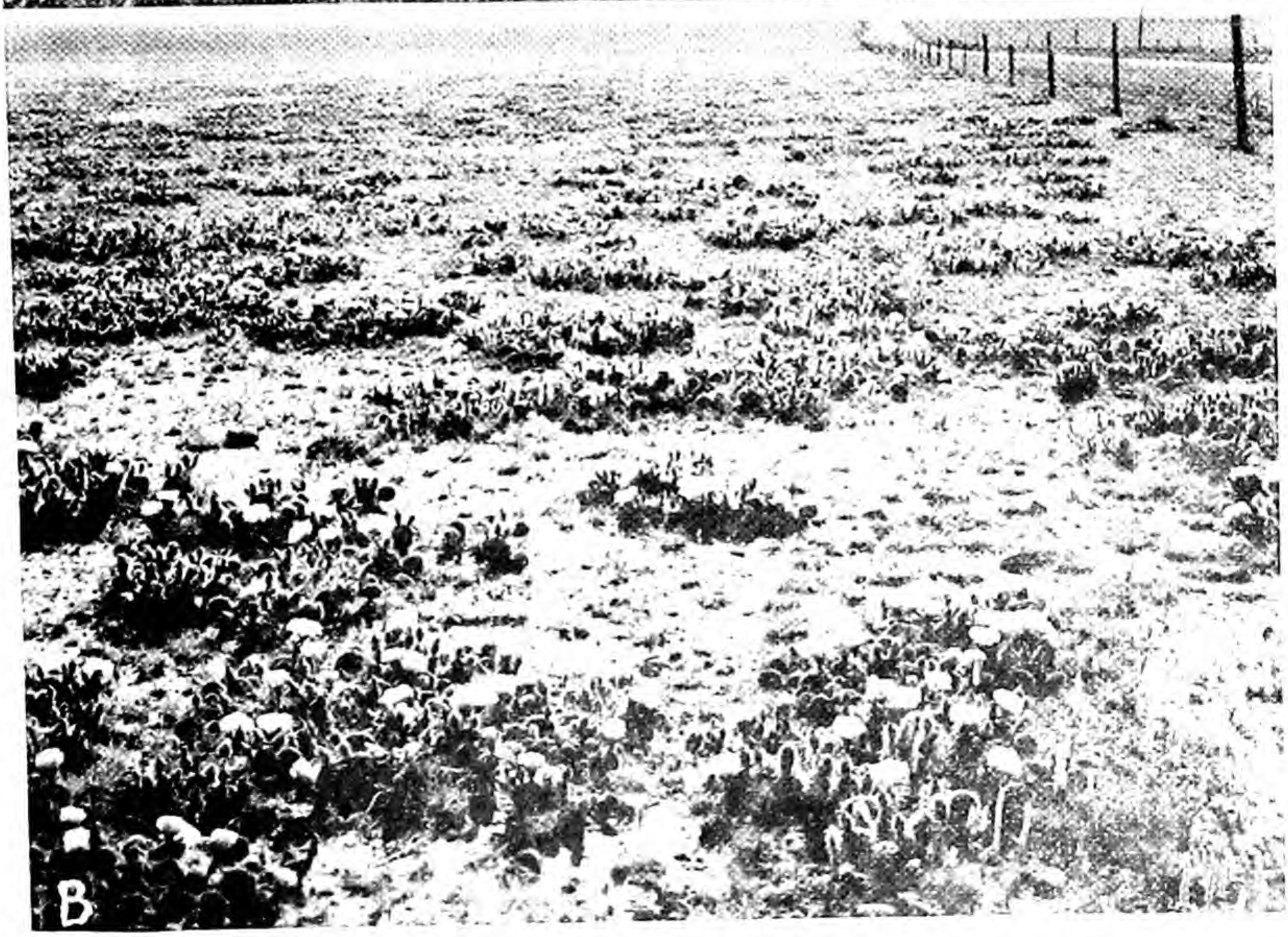
Subclimaxes in the grassland are composed largely of tall grasses, usually in the form of a consocies. In the true prairie, this part is taken by *Spartina cynosuroides* and in the desert plains by *Sporobolus wrighti*, while *Elymus condensatus* plays a similar role in the mixed prairie and in portions of the bunch grass prairies. The function of the tall *Andropogons* is more varied; they are typically postclimax rather than subclimax, though they maintain the latter relation along the fringe of the oak-hickory forest and in oak openings. They occupy a similar position at the margin of the pine subclimax in Texas especially, and hence they are what might be termed "sub-subclimax" in such situations. Beyond the forest and in association with *Elionurus, Trachypogon*, etc., they appear to constitute a faciation of the coastal prairie. Chaparral proper is to be regarded as a climax, but with a change of species it extends into the montane and even the subalpine zone and there constitutes a fire subclimax. In the foothills of southern California, the coastal sagebrush behaves in like manner where it lies in contact with the chaparral.

The disposition of seral stages below the subclimax that exhibit a distinct retardation or halt for a longer or shorter period is a debatable matter. It is entirely possible to include them among subclimaxes, but this would again fail in accuracy and definiteness and hence lead to confusion. The decision may well be left to usage by providing a term for such seral or sub-subclimax communities as persist for a long or indefinite period because of continued or recurrent edaphic control or human disturbance. By virtue of its significance, brevity and accord with related terms, the designation "serclimax" is suggested, with the meaning of a seral community usually one or two stages before the subclimax, which persists for such a period as to resemble the climax in this one respect. For reasons of brevity and agreement, the connecting vowel is omitted, but the *e* remains long as in sere.

For the most part, serclimaxes are found in standing water or in saturated soils as a consequence of imperfect drainage. The universal example is the reed-swamp with one or more of several consocies, such as *Scirpus, Typha, Zizania, Phragmites* and *Glyceria*: this is typical of the lower reaches of rivers, of deltas and of certain kinds of lakes, the great tule swamps of California affording outstanding instances. Another type occurs in coastal marshes in which *Spartina* is often the sole or major dominant, while sedge-swamps have a wider climatic range but are especially characteristic of northern latitudes and high altitudes. The Everglades of Florida dominated by *Cladium* constitute perhaps the most extensive example of the general group, though *Carex* swamps often cover great areas and the grass *Arundinaria* forms jungle-like cane-brakes through the South. Among woody species, *Salix longifolia* is an omnipresent consocies of sand-bars and river-sides, but the most unique example is the cypress-swamp of the South, typified by *Taxodium*. In boreal and subalpine districts the distinctive serclimax is the peat-bog, moor or muskeag, more or less regularly associated with the other seral communities of *Carex* and usually of *Larix* and *Picea* also in the proper region (Plate 39A).

Frequent burning may retard or prevent the development of the normal fire subclimax and cause it to be replaced by a preceding stage. This may be a scrub community or one kept in the shrub form by repeated fires, but along the Atlantic and Gulf Coasts it is usually one of *Andropogon virginicus*, owing to its sufferance of burning. The so-called "balds" of the southern Appalachians are seral communities of heaths or





A. Sereclimax of *Taxodium*, *Nyssa* and *Quercus* forming a cypress swamp, Paris, Arkansas.
B. Disclimax of *Bouteloua*, *Muhlenbergia* and *Opuntia* due to overgrazing of [illegible], Great Plains.

grasses initiated and maintained primarily by fire. Finally, there are serclimaxes of weeds, especially annuals, in cultivated districts, and a somewhat similar community of native annuals is characteristic of wide stretches in the desert region.

Disclimax (Plate 39B).—As with the related concepts, the significance of this term is indicated by a prefix, *dis-*, denoting separation, unlikeness or derogation, much as in the Greek *dys*, poor, bad. The most frequent examples of this community result from the modification or replacement of the true climax, either as a whole or in part, or from a change in the direction of succession. These ensue chiefly in consequence of a disturbance by man or domesticated animals, but they are also occasionally produced by mass migration. In some cases, disturbance and the introduction of alien species act together through destruction and competition to constitute a quasi-permanent community with the general character of the climax. This type is best illustrated by the *Avena-Bromus* disclimax of California, which has all but replaced the bunch grass prairie (Plate 30C).

The grassland climax of North America comprises six well-marked associations (1920, 1929). The mixed prairie, so-called because it is composed of both mid grasses and short grasses, is more or less central to the other five and is regarded as ancestral to them (Plate 49B). To the East along the Missouri and Mississippi Rivers, it has become differentiated into the true prairie formed by other species of mid grasses belonging mostly to the same genera, and this unit is flanked along the western margin of the deciduous forest by a proclimax of tall grasses, chiefly *Andropogon* (Plate 9B). Southward the true prairie is replaced by coastal prairie, which in the main occupies the Gulf region of Texas and Mexico and is constituted by similar dominants but of different species. The desert plains are characterized primarily by species of *Bouteloua* and *Aristida*, which range from western Texas to the edge of the deserts of Mexico and Arizona (Plate 32A). In the Northwest, the short grasses disappear and the palouse prairie of eastern Washington and adjacent regions is formed by mid grasses of the bunch grass life-form, among which *Agropyrum spicatum* is the eudominant (Plate 49A). The same life-form signalizes the California prairie, found from the northern part of the state southward into Lower California, but its special character is derived from endemic species of *Stipa* (Plate 45B).

A similar replacement of endemic grasses by *Bromus tectorum* as

that which has occurred in California, has more recently taken place over large areas of the Great Basin (Plate 36A), while *Poa pratensis* has during the last half-century steadily invaded the native hay-fields and pastures of the true prairie, an advance first noted by Bradbury in 1809. An even more striking phenomenon is the steadily increasing dominance of *Salsola* over range and crop land in the West (Plate 18A), and this is imitated by *Sisymbrium* and *Lepidium* in the Northwest (Plate 31B). It is obvious that all cultivated crops belong in the same general category, but this point hardly requires consideration.

Probably the example most cited in North America is that of the short grass plains, which actually represent a reduction of the mixed prairie due to overgrazing, supplemented by periodic drouth. Over most of this association, the mid grasses, *Stipa, Agropyrum*, etc., are still in evidence, though often reduced in abundance and stature, but in some areas they have been practically eliminated. Similar though less extensive partial climaxes of short grasses characterize pastures in the true, and both pasture and range in the coastal prairie, the dominants regularly belonging to *Bouteloua, Buchloe* or *Hilaria*. Of essentially the same nature is the substitution of annual species of *Bouteloua* and *Aristida* in the desert plains, for perennial ones of the same genera, which is a case of short grasses being followed by still shorter ones.

In other instances, the effect of disturbance is to produce a community with the appearance of a postclimax, when the life-form concerned is that of an undershrub or tall grass. This is notably the case in the mixed prairie when overgrazing is carried to the point of breaking up the short grass sod and permitting the increase of *Artemisia frigida* or *Gutierrezia sarothrae*. In essence, the wide extension of sagebrush (*Artemisia tridentata*) and of creosote bush (*Larrea tridentata*) is the same phenomenon, though only the latter is a climax dominant in its own region. In the case of *Opuntia*, the peculiar life-form suggests an important difference, but the numerous species behave in all significant respects like other shrubs, though with the two advantages of spines and ready propagation.

The communities of tall grasses formed by species of *Andropogon* originally presented some difficulty, since these naturally have all the appearance of a postclimax to the prairie. Probably the greater number are to be assigned to this type, but the evidence from reconnaissance and record indicates that in the true prairie and especially the eastern

portion, *Andropogon furcatus* in particular now constitutes a disclimax due to pasturing, mowing and in some measure to fire also. A characteristic disclimax in miniature is to be found in the "gopher gardens" of the alpine tundra, where coaction and reaction have removed the climax dominance of sedges and grasses to make place for flower gardens of perennial forbs. "Towns" of prairie-dogs and kangaroo-rats often produce similar but more more extensive communities.

Selective cutting not infrequently initiates disclimaxes, as may likewise the similar action of other agents such as fire or epidemic disease. The most dramatic example is the elimination of the chestnut (*Castanea dentata*) from the oak-chestnut canopy, but of even greater importance has been the extreme reduction and fragmentation of the lake forest through the overcutting of white pine. Finally, what is essentially a disclimax may result from climatic mass migration which, in the Black Hills of South Dakota, has brought together *Pinus ponderosa* from the montane climax of the Rocky Mountains and *Picea canadensis* from the boreal forest.

Preclimax and Postclimax.—These related concepts were first advanced in *Plant Succession* (1916, 1928) and have since been discussed in *Plant Ecology* (1929) and in the organization of the relict method (1934). They are both direct corollaries of the principle of the clisere, the spatial series of climaxes that are set in motion by a major climatic shift, like that of the glacial epoch with its opposite phases. The clisere is most readily comprehended in the case of high ranges or summits, such as Pikes Peak where the entire series of climaxes is readily visible, and is what Tournefort described on Mount Ararat in his famous journey of 1700. However, this is but an expression of the continental clisere in latitude, which achieves perhaps its greatest regularity in North America. A similar relation is characteristic of the longitudinal disposition of climaxes in the temperate zone between the two oceans, the portion from deciduous forest through prairie to desert being the most uniform.

With the exception of the two extremes, arctalpine and tropical, each climax has a dual role, being preclimax to the contiguous community of so-called higher life-form and postclimax to that of lower life-form. This may be illustrated by the woodland climax, which is postclimax to grassland and preclimax to montane forest. The arctic and alpine tundras exhibit only the preclimax relation, to boreal and subalpine forest respectively, since a potential lichen climax attains but incomplete expres-

sion northward or upward. While the general primary relation is one of water in terms of rainfall and evaporation, temperature constantly enters the situation and at the extremes may be largely controlling, as in the tundra especially. However, in our present imperfect knowledge of causal factors it is simpler and more definite to determine rank by position in the cliseral sequence, each community higher in altitude or latitude being successively preclimax to the preceding one. This relation is likewise entirely consistent in the clisere from deciduous forest to desert, as it is among the associations of the same climax, though in both these cases the zonal grouping may be more or less obscured.

Wherever concrete preclimaxes or postclimaxes occur, either between climaxes or within a single one, they are due to the compensation afforded by edaphic situations. The major examples of the latter are provided by valleys, especially gorges and canyons, long and steep slope-exposures, and by extreme soil-types such as sand and alkali. The seration is a series of communities produced by a graduated compensation across a valley and operating within a formation or through adjacent ones, while the ecocline embraces the differentiation brought about by shifting slope-exposures around a mountain or on the two sides of a high ridge. In the case of such soils as sand or gravel at one extreme and stiff clay at the other, the edaphic adjustment may sometimes appear contradictory. Thus, sand affords a haven for postclimax relicts in the dry prairie and for preclimax ones in the humid forest region, while the effect of heavy soils is just the reverse. However, this is readily intelligible when one recalls the peculiar properties of such soils in terms of absorption, chresard and evaporation.

Preclimax.—Since they occupy the same general antecedent position with respect to the climax, it is necessary to distinguish with some care between subclimax and preclimax, especially in view of the fact that they often exhibit the same life-form. However, this is not difficult when the priseres and subseres have been investigated in detail, as the actual composition and behavior of the two communities are usually quite different. Moreover, in the first, reaction leads to the entry of the climax dominants with ultimate conversion, while in the second the compensation by local factors is rarely if ever to be overcome within the existing climate, short of man-made disturbance.

Preclimaxes are most clearly marked where two adjacent formations are concerned, either prairie and forest or desert and prairie. Examples

of the first kind are found in the grassy "openings" and oak savannas of the deciduous forest and in the so-called "natural parks" along the margin of the montane and boreal forests (Plate 28B). They are also well developed on warm dry slope-exposures or xeroclines in the Rocky Mountains. In the one, compensation is usually afforded by a sandy or rocky soil, in the other by a local climate due to insolation. Desert climaxes regularly bear the proper relation to circumjacent grassland, but this is somewhat obscured by the shrub life-form, which would be expected to characterize the less xeric formation. This may be explained, however, by the wide capacity for adaptation shown by such plants as *Larrea tridentata* and *Artemisia tridentata,* a quality that is lacking in most of their associates (Plate 37B). Left stranded as relict communities in desert plains and mixed prairie by the recession of the last dry phase, they have profited by the overgrazing of grasses to extend across a territory much larger than that in which they are climax. Here they have all the appearance of a postclimax, especially in the case of *Larrea,* which commonly attains a stature several times that found in the desert. However, since this is the direct outcome of disturbance in terms of grazing, it is better regarded as a disclimax, particularly since the climax grasses still persist in it to some degree (Plate 47A).

Within the same formation, the more xeric associations or consociations are preclimax to the less xeric ones. This is the general relation between the oak-hickory and beech-maple associations of the deciduous forest, the former occupying in the latter the warmer drier sites produced by insolation or type of soil. A similar relation may obtain in the case of faciations, the *Quercus stellata-marilandica* community often being a border of marginal preclimax to the more mesic oak-hickory faciations. Such preclimaxes naturally persist beyond the limits of the association proper as relicts in valleys or sandy soils and then assume the role of postclimaxes to the surrounding grassland, a situation strikingly exemplified in the "Cross Timbers" of Texas. (Plate 51B). In the montane forest of the Rockies, the consociation of *Pinus ponderosa* is preclimax to that of *Pseudotauga taxifolia,* and a similar condition recurs in all forests where there is more or less segregation of consociations.

In the mixed prairie, fragments of the desert plains occur all along the margin as preclimaxes, the most extensive one confronting the Colorado Valley, where it is at the same time postclimax to the desert. The mixed prairie constitutes relicts of this type where it meets the true

prairie. The most frequent examples are provided by *Bouteloua gracilis* and *Sporobolus cryptandrus,* though as with all the short grasses in this role, grazing has played some part.

Postclimax.—As a general rule, postclimax relicts are much more abundant than those that represent preclimaxes, owing in the first place to the secular trend toward desiccation in climate and in the second to the large number of valleys, sandhills and sandy plains, and escarpments in the grassland especially. Postclimaxes of oak-hickory and of their flood-plain associates, elm, ash, walnut, etc., are characteristic features of the true and mixed prairies, holding their own far westward in major valleys but limited as outliers on ridges and sandy stretches to the eastern edge (Plate 40A). However, the compensation afforded by the last two is incomplete as a rule and the postclimax is typically reduced to the savanna type. The latter is an almost universal feature where forest, woodland or chaparral touches grassland, owing to the fact that shrinkage under slow desiccation operates gradually upon the density and size of individuals. Savanna is derived from the reduction of deciduous forest along the eastern edge of the prairie, of the aspen subclimax of the boreal forest along the northern, and of the montane pine consociation, woodland or chaparral on the western and southern borders, recurring again on the flanks of the Sierras and Coast Ranges in California. On the south, the unique ability of the mesquite (*Prosopis juliflora*) to produce root-sprouts after fire, its thorniness, palatable pods and resistant seeds have permitted it to produce an extensive savanna that often closely simulates a true woodland climax. (Plate 27B).

As would be expected, a point is reached in the reduction of rainfall westward in the prairie where sand no longer affords compensation adequate for trees. In general this is along the isohyet of 30 in. in the center and south, and of about 20 in. in the north. Southward from the parallel of 37° the further shrinkage of the oak savanna may be traced in the "shinry," which dwindles from four or five feet to dwarfs only "shin" high. With these are associated tall grasses, principally *Andropogon* and *Calamovilfa* in the form *gigantea*. To the north of this line, the shin oaks are absent and the tall grasses make a typical postclimax that extends into Canada, though the compensatory influence of sand is still sufficient to permit an abundance of such low bushes as *Amorpha, Ceanothus, Artemisia filifolia* and *Yucca*, as well as depauperate hackberry and aspen. In the vast sandhill area of central Nebraska, the tall grass post-

A. Postclimax of *Quercus, Juglans, Ulmus, Fraxinus*, etc.; Canadian River, near Oklahoma City.

B. Postclimax of tall grasses, *Andropogon, Calamovilfa* and *Panicum* in sandhills; Thedford, Nebraska.

climax attains its best development, which is assumed to reflect the climate when the prairies were occupied by the *Andropogons* and their associates some millions of years ago (Plate 40B). The gradual decrease to the rainfall of the present has led to the tall grasses finding refuge in all areas of edaphic compensation, not only in sand but likewise on foothills and in valleys, and in addition along the front of the deciduous forest.

Structure of the Climax

Community Functions.—The nature of community functions and their relation to the structure of climax and sere have been discussed in considerable detail elsewhere, and for the present purpose it may well suffice to emphasize the difference in significance between major or primary and minor or secondary functions. The former comprise aggregation, migration, ecesis, reaction, competition, cooperation, disoperation and coaction, together with the resulting complexes, invasion and succession. Any one of these may have a profound effect upon community structure, but the driving force in the selection and grouping of life-forms and species resides chiefly in reaction, competition, and coaction. Migration deals for the most part with the movement and evolution of units under climatic compulsion, and succession with the development and regeneration of the climax in bare or denuded areas.

In contrast to these stands the group of minor functions that are concerned with numbers and appearance or visibility as it may be termed. The first is annuation, in accordance with which the abundance of any species may fluctuate from dry to wet phases of the various climatic cycles or the growth differ in terms of prominence, the two effects not infrequently being combined. For the grassland, a season of rainfall more or less extreme in either direction often emphasizes one dominant at the expense of others, though the balance is usually redressed by the following year, while in the desert in particular the swing in number of annuals may be from almost complete absence to seasonal dominance, again with one or few species taking the major role. Aspection is mainly the orderly procession of societies through each growing season, more or less modified by changes in number ensuing from annuation. Hibernation and estivation merely affect seasonal appearance and are forms of aspection, with the temporary suspension of coaction effects. While usually applied to the animal members of the biome, it is obvious that plants exhibit certain

responses of similar nature. Diurnation is likewise best known in the case of animals, especially nocturnal ones, but it is exhibited also by the vertical movement of plankton and in different form by the opening and closing of flowers and the "sleep" movements of leaves.

Roles of Constituent Species: Dominants.—The abundant and controlling species of characteristic life-form were long ago termed dominants (1907, 1916), this property being chiefly determined by the degree of reaction and effective competition. In harmony with the concept of the biome, it has become desirable to consider the role of animals likewise; since their influence is seen chiefly in coaction by contrast to the reaction of plants, the term *influent* has been applied to the important species of land biomes (1936). It is an axiom that the life-form of the dominant trees stamps its character upon forest and woodland, that of the shrub upon chaparral and desert, and the grass form on prairie, steppe and tundra. There are seral dominants as well as climax ones, and these give the respective impresses to the stages of prisere and subsere. Finally, there are considerable differences in rank or territory even among the dominants of each formation. The most important are those of wide range that bind together the associations of a climax; to these the term *perdominant* (*per*, throughout) may well be applied. In contrast to these stand the dominants more or less peculiar to each association, such as beech or chestnut in their respective communities and *Sporobolus asper* in the true and *Stipa comata* in the mixed prairie, for which *eudominant* may be employed.

Subdominants regularly belong to a life-form different from that of the dominants and are subject to the control of the latter in a high degree, as the name indicates. They are best exemplified by the perennial forbs, though biennials and annuals may serve as seral subdominants; all three may be actual dominants in the initial stages of succession and especially in the subsere. The term *codominant* has so far had no very definite status; it is hardly needed to call attention to the presence of two or more dominants, since this is the rule in all cases with the exception of consociation and consocies. In contrast to the types mentioned stands a large number of secondary or accessory species that exhibit no dominance, which may be conveniently referred to as *edominants,* pending more detailed analysis.

Influents.—As indicated previously, the designation of *influent* is applied to the animal members of the biome by virtue of the influence or

coaction they exert in the community. The significance of this effect depends much upon the life-form and to a large degree upon the size and abundance of the species as well, and is seen chiefly in the coactions involved in food, material, and shelter. Influents may be grouped in accordance with these properties, or they may be arranged with respect to distribution and role in climax or sere, or to time of appearance (1936). For general purposes it is perhaps most convenient to recognize subdivisions similar to those for dominants and with corresponding terms and significance. Thus, a *perfluent* would occur more or less throughout the formation, while the *eufluent* would be more or less typical or peculiar to an association. *Subfluents* would mark the next lower degree of importance, roughly comparable to that of subdominant, while minute or microscopic influents of still less significance might well be known as *vefluents*.

Climax and Seral Units.—No adequate analysis of vegetation or of the biome is possible without taking full account of development. As the first step, this involves a distinction between climax communities proper and those that constitute the successional movement toward the final stages. The two groups differ in composition, stability, and type of control, but they agree in the possession of dominants, subdominants, and influents. These primary differences made it desirable to recognize two series of communities, viz. climax and seral and to propose corresponding terms, distinguished by the respective suffixes, *-ation* and *-ies* (1916). These have gradually come into use as the feeling for dynamic ecology has grown and bid fair to constitute a permanent basis for all such studies. It is not supposed that they embrace all the units finally necessary for a complete system, but their constant application to the great climaxes of North America for nearly two decades indicates that they meet present needs in the matter of analysis.

Not all communities can be certainly placed in the proper category at the outset, but the number of doubtful cases is relatively small and few of these present serious difficulty under combined extensive and intensive research. This statement, however, presupposes an experience sufficiently wide and long to permit distinguishing between climaxes and the various types of proclimax, as well as recognizing the characteristic features of subclimaxes in particular. Comparative studies over a wide region are indispensable and the difficulties will disappear to the degree that this is achieved. While ecotones and mictia necessarily give rise to

some questions in this connection, these in turn are resolved by investigations as extensive as they are detailed.

Climax Units.—In the organization of these, four types of descending rank and importance were distinguished within the formation, namely, association, consociation, society, and clan. Like the formation itself, the first two were based upon the dominant and its life-form, while the last were established upon the subdominant and its different life-form. It was recognized at the time that the association contained within itself other units formed by the dominants (1920), and two further divisions, *faciation* and *lociation*, with corresponding seral ones, *facies* and *locies*, were suggested and submitted to Prof. Tansley for his opinion as to their desirability. These have been tested in the course of further field studies and have now and then been used in print, though the complete series was not published until 1932. The climax group now comprises the following units, viz. association, consociation, faciation, lociation, society, and clan. At the beginning, it was intended to replace society by *sociation* for the sake of greater uniformity in terms, but the former had attained such usage that the idea was relinquished. However, the use of society in quite a different sense by students of social relations, especially among insects, again raises the question of the desirability of such a substitution, in view of the growing emphasis upon bio-ecology.

Association (Plate 41A).—Under the climax concept this represents the primary division of the biome or formation, and hence differs entirely from the generalized unit of the plant sociologists, for which the term *community* is to be preferred. Each biome consists regularly of two or more associations, though the lake forest and the desert scrub embody two apparent exceptions, each seeming to consist of one association only. However, these are readily explained by the fact that the western member of the former has been obscured by the expansion of montane and coast forests in the Northwest, while one or more additional associations of the desert climax occur to the southward in Mexico, and apparently in South America also.

The number of associations in a particular formation is naturally determined by the number of primary differences and these in turn depend upon the presence of eudominants. Just as the unity of the formation rests upon the wide distribution of several major dominants or perdominants, so the association is also marked by one or more dominants peculiar to it, and often as well by differences in the rank and grouping

A. Association of mixed prairie, *Stipa, Agropyrum, Bouteloua*, etc.; Monument, Colorado
B. Foothill faciation of the desert-plains association, *Bouteloua eriopoda, B. gracilis, B. hirsuta, B. filiformis*, etc.; Safford, Arizona

of dominants held in common. Thus, in the true prairie association, the eudominants are *Stipa spartea, Sporobolus asper* and *heterolepis;* for the desert plains *Bouteloua eriopoda, rothrocki* and *radicosa* and *Aristida californica,* while *Stipa comata* and *Buchloe* take a similar part in the mixed prairie. In the deciduous climax, the characteristic dominants of one association are supplied by the beech and hard maple, of a second by chestnut and chestnut-oak, though the oak-hickory association, of wider range and greater complexity, is comparatively poor in eudominants by contrast with the number of species.

The structural and phyletic relations of the associations of a climax are best illustrated by the grassland, which is the most highly differentiated of all North American formations, largely as an outcome of its great extent. The most extensive and varied unit is the mixed prairie, which occupies a generally median position with respect to the other five associations of this climax (Plate 41A). Originally, it derived its dominants from three separate regions, *Stipa, Agropyrum* and *Koeleria* coming from Holarctica, *Sporobolus* from the South, and the short grasses from the Mexican plateaus, and it still exhibits the closest kinship with the Eurasian steppe. It contains nearly all the genera that serve as dominants in the related associations, while many of the eudominants of these have all the appearance of direct derivatives from its species, as is shown by *Stipa, Sporobolus, Poa,* and *Agropyrum.* The evolution of both species and communities is evidently in response to the various subclimates, that of the true prairie being moister, of the coastal warmer as well; the desert plains are hotter and drier, the California prairie marked by winter rainfall and the Palouse by snowfall.

Consociation.—In its typical form the consociation is constituted by a single dominant, but as a matter of convenience the term is also applied to cases in which other dominants are but sparingly present and hence have no real share in the control of the community. It has likewise been convenient to refer in the abstract to each major dominant of the association as a consociation, though with the realization that it occurs more frequently in mixture than by itself. In this sense it may be considered a unit of the association, though the actual area of the latter is to be regarded as divided into definite faciations. Consociation dominants fall into a more or less regular series with respect to factor requirements, especially water content, and often exhibit zonation in consequence. This is a general feature of mixed prairie where *Agropyrum*

smithi and *Stipa comata* are the chief mid grasses, the former occupying swales and lower slopes, the latter upper slopes and ridges.

The consociation achieves definite expression over a considerable area only when the factors concerned fluctuate within the limits set by the requirements of the dominant or when the other dominants are not found in the region. The first case may be illustrated by *Pinus ponderosa* in the lower part of the montane forest and by *Adenostoma fasciculatum* in the Sierran chaparral, while the second is exemplified by *Picea engelmanni* in the Front Range of Colorado, its usual associate, *Abies lasiocarpa,* being absent from the district. In rolling terrain like that of the prairie, each consociation will recur constantly in the proper situation but is necessarily fragmentary in nature. Such behavior is characteristic of dominants with a postclimax tendency, as with *Stipa minor* and *Elymus condensatus* in swales and lower levels of the mixed prairie.

Faciation (Plate 41B).—This is the concrete subdivision of the association, the entire area of the latter being made up of the various faciations, except for seral stages or fragments of the several consociations. Each faciation corresponds to a particular regional climate of real but smaller differences in rainfall, evaporation and temperature. It may be characterized by one or two eudominants, such as *Hilaria jamesi* and *Stipa pennata* in the southern mixed prairie, but more often it derives its individuality from a sorting out or a recombination of the dominants of the association. As is evident, the term is formed from the stem *fac-*, show, appear, as seen in *face* and *facies,* and the suffix *-ation,* which denotes a climax unit.

During the past decade, much attention has been given to the recognition and limitation of faciations on the basis of the presence or absence of a eudominant, such as *Hilaria, Buchloe,* or *Carex,* or a change in the rank or grouping of common dominants, like *Stipa, Agropyrum, Sporobolus* or *Bouteloua.* In the prairie this task has been complicated by overgrazing, cultivation and related disturbances, while selective lumbering and fire have added to the difficulties, in the deciduous forest especially. In general, temperature appears to play the leading part in the differentiation of faciations, since they usually fall into a sequence determined by latitude or altitude, although rainfall/evaporation is naturally concerned also. The mixed prairie exhibits the largest number, but it is approached in this respect by the deciduous forest as a consequence of wide extent and numerous dominants. Over the Great Plains from north to south,

the successive faciations are *Stipa-Bouteloua, Bouteloua-Carex, Stipa-Agropyrum-Buchloe, Bouteloua-Buchloe, Hilaria-Stipa-Bouteloua,* and *Agropyrum-Bouteloua.* However, the short grass communities are to be regarded as disclimaxes wherever the mid grasses have been eliminated or nearly so, a condition that fluctuates in relation to dry and wet phases of the climatic cycle.

Lociation.—In its turn, the lociation is the subdivision of the faciation, the term being derived from *locus,* place, as indicating a general locality rather than a large region. Nevertheless, a lociation may occupy a relatively extensive territory up to a hundred miles or more in extent, by comparison with several hundred for the faciation. It is characterized by more or less local differences in the abundance and grouping of two or more dominants of the faciation. These correspond to considerable variations in soil, contour, slope-exposure or altitude, but all within the limits of the faciation concerned. As a consequence, lociations are very often fragmented, recurring here and there as alternes with each other, and frequently with proclimaxes of various types. Like most climax units, they have been modified by disturbance in some degree, and this fact must be constantly kept in mind in the task of distinguishing them from subclimax or disclimax.

A detailed knowledge of the faciation is prerequisite to the recognition of the various lociations in it. The number for a particular faciation naturally depends upon the extent of the latter and the number of dominants concerned. Consequently, lociations are more numerous in the faciations of the mixed prairie and desert plains, of the chaparral and the oak-hickory forest. As would be expected, they are often most distinct in ecotones and in districts where there is local intrusion of another dominant. In correspondence with their local character, it is important to eliminate or diminish superimposed differences through restoration of the original cover by means of protection enclosures and thus render it possible to disclose the true composition.

Society.—This term has had a wide range of application, but by dynamic ecologists it has generally been employed for various groupings of subdominants, of which those constituted by aspects or by layers are the most important. In addition, there are a great many minor communities formed by cryptogams in the ground layer or on host-plants and other matrices. The soil itself represents a major layer, divisible into more or less definite sublayers. Animals regularly assume roles of vary-

ing importance in all of these, especially the insects, subdominant plants and subinfluent animals. It is doubtful whether animals form true societies independently of their food-plants or those used for materials or shelter, but this is a question that can be answered only after the simplest units, namely, family and colony, have been recognized and coordinated in terms of their coactions.

In view of what has been said previously, it seems desirable to employ society as the general term for all communities of subdominants and subinfluents above the rank of family and colony, much as community is the inclusive term for all groupings of whatsoever rank. This then permits carrying out the suggestion made in 1916 that the major types of societies be set apart by distinctive names. In accordance, it is here proposed to call the aspect society a *sociation* and the layer society a *lamiation*, while the corresponding seral terms would be *socies* and *lamies*. Many of the societies of cryptogams and minute animals would find their place in these, particularly so for those of the surface and soil layers, but many others take part in a miniature sere or *serule*, such as that of a moldering log, and may best receive designations that suggest this relation.

Sociation (Plate 42A).—Wherever societies are well developed, they regularly manifest a fairly definite seasonal sequence, producing what have long been known as aspects (1898). As phenomena of the growing season, these were first distinguished as early spring or prevernal, vernal proper, estival and serotinal or autumnal, but there may also be a hiemal aspect, especially for animals, in correspondence with an actual and not merely a calendar winter as in California.

Sociations are determined primarily by the relation between the life cycle of the subdominants and the seasonal march of direct factors, temperature in particular. So far as the matrix of plants is concerned, the constituent species may be in evidence throughout the season, but they give character to it only during the period of flowering, or fruiting in the case of cryptogams. They are present largely or wholly by sufferance of the dominants, and they are to be related to the reactions of these and competition among themselves rather more than to the habitat factors as such. In grassland and desert, they are often more striking than the dominants, sometimes owing to stature but chiefly as an effect of color and abundance, and they may also attain much prominence in woods where the canopy is not too dense.

Sociations are usually most conspicuous and best developed in grassland, four or even five aspects occurring in the true prairie from early

A. Societies of [illegible] and [illegible], autumnal aspect, Belmont Prairie, Lincoln, Nebraska.
B. [illegible] of [illegible] ([illegible], *Pilea*, [illegible], *Impatiens*, etc.), in Oak-Hickory forest.

spring to autumn. In the mixed prairie these are usually reduced to three, and in the desert plains and desert proper, two major ones, summer and winter, in which however there may be subaspects marked by *sations*, as indicated later. Short seasons due to increasing latitude or altitude afford less opportunity, and the tundra, both alpine and arctic, usually exhibits but two aspects, the sociations however taking a conspicuous role as in the prairie. In woodland the number and character of the sociations depend largely upon the nature of the canopy, and for deciduous forest the flowery sociations regularly belong to the spring and autumn aspects, when the foliage is either developing or disappearing.

It is convenient to distinguish sociations as simple or mixed with respect to the plant matrix in accordance with the presence of a single subdominant or of two or more. However, when animals are included in the grouping, such a distinction appears misleading and may well be dropped. The word "mixed" would be more properly applied to plant-animal societies were it not for the fact that this appears to be the universal condition. Since seasonal insects are legion, many of the societies in which they take part are best denoted as *sations*.

Lamiation (Plate 42B).—The term for a layer society is derived from the stem *lam-* seen in lamina and lamella. As is well known, layers are best developed in forests with a canopy of medium density, so that under the most favorable conditions as many as five or six may be recognized above the soil. In such instances, there are usually two shrub stories, an upper and lower, often much interrupted, followed by tall, medium and low forb layers, and a ground community of mosses, lichens and other fungi, and usually some delicate annuals. The soil population is perhaps best treated as a single unit, though it may exhibit more or less definite sublayers. When the various layers beneath the dominants are distinct, each is regarded as a lamiation, but in many cases only one or two are sufficiently organized to warrant designation, e.g., shrub or tall-herb lamiation.

Layers are often reduced to a single lamiation of low herbs in the climax forest, especially of conifers, and even this may be entirely lacking in dense chaparral. Two or three layers of forbs may be present in true prairie in particular, the upper lamiation being much the most definite and often concealing the grass dominants in the estival aspect, but the structure of grassland generally reflects the greater importance of sociations. Sagebrush and desert scrub exhibit no proper lamiations,

owing to the interval between the individual dominants, but the herbaceous societies of the interspaces show something of this nature.

As a rule, well-developed lamiations also manifest a seasonal rhythm, corresponding to aspects or to subaspects. These constitute recognizable groupings in the lamiation and for the sake of determination and analysis may be termed *sations*. This word is a doublet of season, both being derived from the root *sa-*, sow, hence grow or appear. Because of the frequent interplay of aspects and layers, the sation may for the present be employed for the subdivision of both sociation and lamiation, and especially where seasonal species of invertebrates play a conspicuous role.

Clan.—This is a small unit of subordinate importance but commonly of distinctive character. It is marked by a density that excludes all or nearly all competing species, in consequence of types of propagation that agree in the possession of short offshoots. Extension is usually by bulb, corm, tuber, stolen or short rootstock, each of which produces a more or less definite family grouping; in fact, most clans are families developed in the climax matrix and sometimes with a blurred outline in consequence. Clans of a particular species such as *Delphinium azureum* or *Solidago mollis* are dotted throughout the respective sociation, often in large numbers, and contribute a distinctive impress much beyond their abundance. Like all units, but small ones especially, they are subject to much fluctuation with the climatic cycle, as a result of which they may pass into societies or be formed by the shrinkage of the latter.

Seral Units.—The concepts of dominance and subdominance apply to the sere as they do to the climax, as does that of influence also, and the corresponding sets of units bear the same general relation to each other. Each of the four major units is the developmental equivalent of a similar community in the climax series and this is likewise true of the various kinds of societies. They constitute the successive stages of each sere, both primary and secondary, including the subclimax, where they often achieve their best expression. It has also been customary to employ seral terms for preclimax and postclimax, and this appears to be the better usage for disclimax and proclimaxes in general. From the fragmentary nature of bare areas and suitable water bodies in particular, seral communities are often but partially developed and one or more units will be lacking in consequence. Thus, the reed-swamp associes is frequently represented by a single one of its several consocies and the minor units are even more commonly absent.

The associes is the major unit of every sere, the number being rela-

tively large in the prisere and small in the subsere. The universal and best understood examples are those of the hydrosere, in which *Lemna, Potamogeton, Nuphar, Nymphaea, Nelumbo,* and others form the consocies of the floating stage, and *Scirpus, Typha, Phragmites,* etc. are the dominants of the reed-swamp or amphibious associes. As already indicated, every consocies may occur singly and often does when the habitat offers just the proper conditions for it or the others have failed to reach the particular spot. When the ecial range is wider, various combinations of two or three dominants will appear, to constitute corresponding facies. Locies are less definitely marked as a rule, except in swamps of vast extent, but are to be recognized by the abundance of reed-like dominants of lower stature, belonging to other species of *Scirpus,* to *Heleocharis, Juncus,* etc. Both facies and locies seem to be better developed in sedge-swamp with its larger number of dominants, though the Everglades with the single consocies of *Cladium* form a striking exception.

The tree-swamps of the southeastern United States contain a considerable number of consocies, such as *Taxodium distichum, Nyssa aquatica, biflora* and *ogeche, Carya aquatica, Planera aquatica, Persia palustris* and *borbonia, Magnolia virginiana, Fraxinus pauciflora, profunda* and *caroliniana,* and *Quercus nigra.* These are variously combined in several different facies, though a more detailed and exact study of the swamp sere may show the presence of two woody associes, distinguished by the depth or duration of the water. As with other scrub communities, the heath associes of peat-bog and muskeag comprises a large number of dominants and presents a corresponding wealth of facies and locies.

In the hydrosere of the deciduous forest, the typical subclimax is that of the flood-plain associes, composed of species of *Quercus, Ulmus, Fraxinus, Acer, Betula, Juglans, Celtis, Platanus, Liquidambar, Populus* and *Salix* for the most part. There are at least three well-marked facies, namely, northern, central and southern, each with a number of more or less distinct locies. The swamp associes or subclimax of the lake and boreal forests consists of *Larix laricina, Picea mariana, Thuja occidentalis,* occurring often as consocies but generally in the form of zoned facies. A large number of fire subclimaxes appear in the form of consocies, as with many of the pines, but associes are frequent along the Atlantic Coast, as they are in the boreal climax, where aspens and birches are chiefly concerned. The number of shrubs and small trees that play the part of seral dominants in the deciduous climax is much larger, producing not

only a wide range of associes but of facies and locies as well. More than a dozen genera and a score or so of species are involved, chief among them being *Sassafras, Diospyrus, Asimina, Hamamelis, Prunus, Ilex, Crataegus* and *Robinia*. The subclimax of the xerosere is constituted for the most part by species of *Quercus*, forming an eastern, a southeastern and a western associes, the last with two well-marked facies, one of *stellata* and *marilandica*, the other of *macrocarpa* and *Carya ovata*.

Among postclimax associes, those of grassland and scrub possess a large number of dominants and exhibit a corresponding variety of facies and locies, together with fairly definite consocies. In the sandhills of Nebraska, the tall grasses concerned are *Andropogon halli, furcatus* and *Sorghastrum nutans, Calamovilfa longifolia, Eragrostis trichodes, Elymus canadensis* and *Panicum virgatum;* some of these drop out to the northward and others to the south, thus producing at least three regional facies. The mesquite-acacia associes of the Southwest possesses a larger number of dominants and manifests a greater variety of facies through its wide area, and this is likewise true of the coastal sagebrush of California.

With reference to seral societies, it must suffice to point out that these are of necessity poorly developed in the initial stages of both hydrosere and xerosere, as the dominants are relatively few. Even in the reed-swamp, true layers are the exception, being largely restricted to such subdominants as *Alisma, Pontederia, Hydrocotyle,* and *Sagittaria*, which are found mostly in borders and intervals. However, in extensive subclimaxes and postclimaxes the situation is quite different. The tall grass associes of sandhills is often quite as rich in saties and lamies as the true prairie, while the various subclimaxes of the several great forest types may equal the latter in the wealth of subdominants for each season and layer, the actual communities being very much the same.

Serule.—This term, a diminutive of *sere*, has been used for a great variety of miniature successions that run their short but somewhat complex course within the control of a major community, especially the climax and subclimax. They resemble ordinary seres in arising in bare spots or on matrices of different sorts, such as earth duff, litter, rocks, logs, cadavers, etc. Parasites and saprophytes play a prominent and often exclusive role in them, and plants and animals may alternate in the dominant parts. The organisms range from microscopic bacteria and worms to mites, larvae, and imagoes on the one hand and large fleshy and shelf fungi on the other. The most important of these in terms of coaction and abundance are known as *dominules* (1936), with *sub-*

dominule and *edominule* as terms for the two degrees of lesser importance. On the same model are formed *associule, consociule,* and *sociule* in general correspondence with the units of the sere itself. In addition there are families and colonies of these minute organisms, which are essentially similar to those of the initial stages of the major succession. Up to the present, little attention has been devoted to the development and structure of serules, but they are coming to receive adequate consideration in connection with bio-ecological problems. Many of the coactions, however, have long been the subject of detailed research in the conversion of organic materials.

Rank and Correspondence of Units

The following table exhibits the actual units of climax and sere, as well as their correspondence with each other. However, for the complete and accurate analysis of a great climax and especially the continental mass of vegetation, it is necessary to invoke other concepts, chiefly that of the proclimax and of communities mixed in space or in time. The several proclimaxes have already been characterized and the eocline and seration briefly defined. To these are to be added the *ecotone* and *mictium,* both terms of long standing, the former applied to the mixing of dominants between two units, the latter to the mixed community that intervenes between two seral stages or associes. Finally, there will be the several types of seres in all possible stages of development, the prisere in the form of hydrosere, xerosere, halosere or psammosere in regions less disturbed and a myriad of subseres in those long settled.

Table of Climax and Seral Units

	Eoclimax	
	Panclimax	
Climax		*Sere*
	Climax (Formation)	
Association		Associes
Consociation		Consocies
Faciation		Facies
Lociation		Locies
Sociation	*Serule*	Socies
Lamiation		Lamies
Sation	Associule	Saties
Clan	Consociule	Colony
	Sociule	Family

As indicated previously, the word *community* is employed as a general term to designate any or all of the preceding units, while *society* may well be used to include those of the second division, i. e. sociation, etc. These are characterized by subdominants in contrast to the dominants that mark the first group. It has also been pointed out that the entire area of the association is divided into faciations and that the consociation is the relatively local expression of complete or nearly complete dominance on the part of a single species. The clan corresponds to the family as a rule, but in some cases resembles the colony in being formed of two species. Families and colonies may also appear in climax communities but this is regularly in connection with the serule.

Panclimax and Eoclimax.—The comprehensive treatment of these concepts is reserved for later consideration, but it is desirable to characterize them briefly here. The *panclimax* (*pan*, all, whole) comprises the two or more related climaxes or formations of the same general climatic features, the same life-form and common genera of dominants. The relationship is regarded as due to their origin from an ancestral climax or *eoclimax* (*eos*, dawn) of Tertiary or even earlier time, as a consequence of continental emergence and climatic differentiation. In the past, eoclimaxes formed a series of great biotic zones in the northern hemisphere with the pole as a focus, and this zonal disposition or clisere is still largely evident in the arrangement of panclimaxes at the present. It is striking in the case of the arctic tundra and taiga or boreal forest, fairly evident for deciduous forest and prairie-steppe, and somewhat obscure for woodland and chaparral-macchia, while the position of deserts is largely determined by intervening mountain ranges. This is true likewise of grassland in some degree, and taken with the former broad land connection between North and South America explains why both prairie and desert panclimax contain at least one austral formation.

In the light of what has been said earlier, it is readily understood that panclimax and panformation are exact synonyms, as are eoclimax and eoformation. Panbiome and eobiome are the corresponding terms when the biotic community is taken as the basis for research.

Prerequisites to Research in Climaxes.—It would be entirely superfluous to state that the major difficulty in the analysis of vegetation is its complexity, were it not for the fact that it is too often taken as the warrant for the static viewpoint. This was embodied in the original idea of the formation as a unit in which communities were assembled on a

physiognomic basis, quite irrespective of generic composition and phyletic relationship. It is not strange that this view and its corollaries should have persisted long past its period of usefulness, since this is exactly what happened with the artificial system of Linnaeus, but the time has come to recognize fully that a natural system of communities must be built just as certainly upon development and consequent relationship as must that of plant families. Complexity is an argument for this rather than against it, and especially in view of the fact that the complexity discloses a definite pattern when the touchstone of development is applied to it.

Though the mosaic of vegetation may appear to be a confusing patchwork in countries long occupied by man, the changes wrought upon it are readily intelligible in terms of the processes concerned. As emphasized previously, the primary control is that of climate, in a descending scale of units that correspond to formation, association, and faciation. Upon this general pattern are wrought the more circumscribed effects of physiography and soil, and both climatic and edaphic figures are overlaid and often more or less completely obscured with a veneer applied by disturbance of all possible kinds. Even above this may be discerned the effect, transient but nonetheless apparent, of such recurrent changes as annuation and aspection. Moreover, the orderly pattern of climate is complicated by great mountain ranges so that such climaxes as tundra and taiga occur far beyond their proper zone, and the effect is further varied by the relative position of the axis.

The migrations of climaxes in the past are a prolific source of fragmentary relicts, the interpretation of which is impossible except in terms of dynamics. This is likewise true of savanna, which represents the shrinkage of forest and scrub under a drying climate and is then further modified by fire or grazing. Fragmentation from this and other causes is characteristic of every diversified terrain and reaches its maximum when human utilization enters the scene upon a large scale. Somewhat similar in effect though not in process is the reduction of the number of dominants by distance, with the consequence that an association of several may be converted into a consociation of one. Such a shrinkage naturally bears some relation also to climate and physiography, especially as seen in the glacial period, and finds its best illustration in the general poverty of dominants in the coniferous and deciduous climaxes of Europe, by contrast with those of eastern Asia and North America. A similar contrast obtains between the grassland of Asia and of North America, the

latter being much richer in dominants, while South America approximates it closely in this respect.

On the part of the investigator, the difficulties in the way of an extensive and thoroughgoing study of climaxes are usually more serious. They arise partly from the handicap too often set by state or national boundaries and partly from the limitations of funds and time. They are also not unrelated to the fact that it is easiest to know a small district well and to assume that it reflects larger ones with much fidelity. As a consequence, it is impossible to lay too much stress upon the need for combining intensive and extensive methods in the research upon climaxes, insofar as their nature, limits and structures are concerned. The detailed development in terms of primary and secondary succession lends itself much more readily to local or regional investigation, but even here a wider perspective is essential to accurate generalization.

Chapter V

THE RELICT METHOD IN DYNAMIC ECOLOGY

Introduction

A large part of our national interest is being directed toward restoring western grazing lands to their original productive condition. Climax plant communities are the supreme expression of the local climate and soil, but over most of the land these climaxes have been modified by grazing, plowing and lumbering, or other activities of man. As a result, only fragments of the original plant cover remain as clues to what had existed under natural conditions in the past, and as indicators for its restoration in the future. By discerning interpretation of these relict plant communities, the former climax can be reconstructed and furnish a guide to successful agriculture, reforestation, and progressive range management.

Without knowledge of the potentialities of the land, its complete utilization may be overlooked as may be illustrated by the presence of short grasses over a large part of the prairies of the United States. That this region originally supported a cover of tall and mid grasses as the natural climax vegetation is evidenced not only by the relicts remaining in protected spots, but by the reports of early explorers and travelers who had the opportunity of viewing it before the advent of settlers. A knowledge of this condition has great economic significance, since it leads to the restoration of the taller grasses which are 25-50% more efficient for grazing purposes than the disclimax of short grasses that has resulted from the elimination of the tall grasses under too great grazing pressure.

The recognition and development of the relict method in the reconstruction of vegetation in North America have been due to the unique advantages offered by this continent. These result not alone from its great extent in latitude, a feature that it shares with Asia, but also from the roughly parallel coast-lines and in particular the three far-flung cordilleras stretching from the Arctic to the Tropics or Subtropics. Both coast and mountain introduce a regularity in variation without a rival elsewhere, and one that is unsurpassed in yielding values for comparison and contrast. Further striking features are the juxtaposition of the

highest accessible mountain (14,500 ft.) and the deepest trough (396 ft. below sea-level) within 50 miles of each other, and mean rainfalls of 100 and 1 inch within a few hundred miles.

As to the vegetation itself, the variety and extent of climaxes is unequalled, and the operation of glacial pulsations on these, not to be matched outside of Europe. The great grassland formation is without a peer in its continuity and differentiation, and nowhere else is such a vast climax in contact with so many others of diverse character. Further, the deciduous forest of the East clothed a territory larger by far than that of eastern Asia, with a list of dominants quite beyond comparison. What is true of climaxes holds equally for climates, with the consequence that no other region of the globe possesses such an opportunity for tracing the causal relation between the two.

Turning to dynamic features, North America is not surpassed in the number of lakes and mountain ranges that afford bare areas for hydrosere and xerosere. Even more characteristic is the number of coastal, river, and inland dune areas, and the wide extent of "badlands." However, it is in connection with the secondary succession that this continent stands pre-eminent. This is due in part to the features already enumerated, but chiefly to the fact that it occupies a median position between Eurasia and the austral continents with respect to its conquest by man. The latter has not been in possession sufficiently long to have modified profoundly the natural vegetation, as in Europe and much of Asia, and yet his influence has been more marked and extensive than over most of the area of other continents. Even more significant has been the wave-like migration of population to the westward, with the result that man and his processes have left a graduated record of the changes wrought, a scale of effects of the first importance to dynamic ecology.

The first contact with the outstanding changes of North American vegetation revealed the significance of drouth periods and overgrazing for the interpretation of the structure of grassland, in the course of a 200 mile reconnaissance along the Missouri and Niobrara rivers in Nebraska in 1893. Similar expeditions further to the west at the end of the protracted drouth, in 1896-8, confirmed the significance of the dynamic approach, and this was embodied in the first treatise on this theme in 1901. Since that time, the dynamic method has been developed in great detail and tested year after year in the widest range of vegetation. Certain major features of it have been made available from time to time (1905, 1916,

1920), but it seems desirable to present a comprehensive and usable account of the detailed technique herewith.

With development as the key to vegetation and later to the biome, it became obvious that a study of the actual community at a particular time and place could yield only a static picture. Though a knowledge of "what is on the ground" is both indispensable and prerequisite, by itself it represents but a segment of the dynamic flow of processes. Taken alone, its facts are deficient in meaning or actually misleading, and it is solely by placing them in the proper setting as to time and events that they gain their true significance. With vegetation as with life in general, it is an axiom that the present is the heir to the past and the forerunner of the future, but an axiom that lies at the very foundation of ecology. This is merely a figurative expression of the principle that causes produce effects and these in turn may become causes, the cardinal tenet of ecology by virtue of its very name. In brief, the understanding of existing vegetation cannot proceed out of itself alone, and one must turn to causes and processes for its interpretation, as well as to forecast the course of its future development or its fate.

Field Methods.—Ecological methods for the field fall into four major categories, namely: (1) measurement by means of instrument, phytometer and quadrat; (2) development, community functions and especially the complex process of succession; (3) experiment in terms of exclosures, transplants and field controls, and (4) indicators, which contain values derived from all of these in terms of nature's experiments. The present treatment is concerned directly with the last and through this with all the others, since it lends itself readily to observation and reconnaissance. However, the method of indicators must be on the one hand fully synthetic and on the other both detailed and comprehensive to yield objective results of permanent value. It cannot be applied with safety or accuracy to a local area alone, nor can it transmute the observations of hasty reconnaissance into dependable results. As always in ecological studies, the extensive must be refined by the intensive, and the latter in turn carried into other areas and regions to secure adequate tests of its general trustworthiness. In consequence, these researches which cover a period of forty years, have combined intensive work at four bases—Lincoln, Pikes Peak, Tucson and Santa Barbara—with extensive reconnaissance of approximately half-a-million miles, with the result that many regions have been studied again and again.

The repetition involved is an indispensable feature of thoroughgoing field technique, by virtue of three major reasons. The first is that it permits examining each community in the entire round of the seasons, a matter of prime importance for studying the dominants and subdominants of grassland in particular, many of which are visible and important only during the proper aspect. The second and even more significant is the striking difference from year to year in consequence of the effect of plus and minus phases of the climatic cycle, as exemplified in the process of annuation. For example, when first visited in 1893 at a time of sunspot maximum and drouth, the grassland of the Niobrara region was composed chiefly of short grasses; at a later visit in 1915, a period of sunspot minimum and excessive rainfall, these were entirely secondary to the mid grasses of the mixed prairie. A third reason, of especial import in the present connection, is the progressive nature of man's coactions upon vegetation and fauna, often complicated by the cessation of a particular activity and process, or even by its reversal. Most significant of all is the fact that the interaction of all these climatic and human processes imparts to the biome a quasi-experimental value that is often not to be matched by actual experiments. Such natural examples are so numerous and varied as to constitute incomparable material for comparison and interpretation.

Materials and Obectives.—The indicator method and its applications have been discussed in comprehensive fashion in *Plant Indicators,* and less extensively in *Plant Succession and Indicators,* so that it will suffice to point out here merely the general relations. Dominant and subdominant, climax and sere in both structure and development, are all eloquent indicators of factor or process, and hence of past events and of future changes in the biome. The basic relation is that of the species-individual or specient to its habitat, and all indicator values are derived in the last analysis from the closeness of this bond. It explains the orderly progession of succession under the control of climate, as well as deviation from it, and also the temporary or permanent modifications due to climatic pulsations. It is the indicators of physical factors in terms of climate and soil, of water, heat, light, solutes, etc., and of such complexes as altitude, slope exposure, and erosion that serve as the basis for unraveling the various functions of the community, such as reaction, competition, coaction, and the many processes by which man in particular modifies it, by virtue of burning, clearing, cultivating, fencing,

grazing, or draining. For the present purpose, these fall into two major groups, namely, climatic indicators such as preclimax, postclimax and clisere, and edaphic ones of disturbance, viz. proclimax, subclimax, and subsere especially. However, all these have in common the fact that they owe their significance to their position in a cause-effect sequence leading from the past to the present and forward into the future.

Method of Relicts

Nature of Relicts.—In the ecological sense, a relict is a community or fragment of one that has survived some important change, often to become in appearance an integral part of the existing vegetation. Thus, the hemlock (*Tsuga canadensis*) constitutes relict groups in the maple-beech forest of the eastern United States; the tall *Andropogons* are relicts in the sandhills of Nebraska, and the grasses bear a similar relation to the desert scrub of Death Valley. Obviously, the term may be applied also with equal warrant to the individual or the species, but it is a practically universal rule that a community of some degree is concerned. Though it may be employed properly for laggards in the course of succession, its most significant use is in connection with climaxes and these naturally furnish the most striking examples of it.

It is evident that relicts possess two indicator values of the first importance. These relate to the causes concerned on the one hand and to the original vegetation and its changes on the other. The former may be climatic, edaphic, or human; each exhibiting a more or less distinctive impress. Climatic causes operate primarily upon the climax, with the widespread destruction of the existing community and the mass migration of the complementary one as the outstanding effects, illustrated by the replacement of grass by scrub in the Mohave Desert (Plate 43A). Edaphic causes are expressed largely in succession, relicts being conspicuous only when the denuding process is more or less partial. Human agencies are characteristically destructive and their operation is naturally most frequent over the wide stretches of climax, or subclimax after these are once established. The consequent relicts occur and recur in endless number, and supply an unlimited opportunity for the investigation of natural experiments in development.

In accordance with the preceding, the presence of a relict community indicates the operation of a compensatory or protective feature.

A. Climatic relicts of *Hilaria, Stipa, Aristida* and *Oryzopsis* on rocky slopes; Death Valley, California.

B. Relict area of *Stipa* consociation; suburbs of Colorado Springs, Colorado.

In the case of a dry phase of the climatic cycle, the compensation for reduced rainfall may be provided by altitude, by northerly slope exposure or a sandy soil. With new or denuded areas, the determining feature may be elevation or a barrier, as in flooding or lava flows, the location of channels in the case of draining, or the force and direction of the wind, as exemplified by the drifting of dune sand or the running of fire. The relicts due to human agency, directly or indirectly, are consequences of protection in various forms, except in the rarest instances. Such protection may be purposeful, but in the newer continents especially it is chiefly accidental, involving the widest range of choice and object. Conservation in fact is primarily a change from the accidental to the intentional protection of communities; in other words it is chiefly the preservation and extension of relicts. Protection assumes a variety of forms, of which fencing and fire lines are the most universal, though it is not infrequently inherent in plant or group. However, it is obvious that protection by fencing applies only to exclosure, since enclosure in varying degree may lead to profound modification, or even to complete destruction in corrals.

The location of relicts will be largely determined by the process concerned. Climatic relicts are typical of the ecotones between formations or associations, and in particular of dissected regions along the front of broad movements. They also occur not infrequently in the heart of great climax areas, where outlier, canyon, or sand provides the necessary compensation. Relicts due to man's activities follow or reflect more or less closely the location and frequency of the latter. Forest relicts mark the course of lumbering and fire, those produced by cultivation characterize farming regions, and those consequent upon grazing are mostly to be found in peripheral grasslands, while the effects of construction are usually localized about cities, towns, and highways.

Shrinkage of Climaxes.—The special study of relict communities in North America for nearly two decades has led to the conclusion that effective migration is by climax masses under the compulsion of climatic changes, and this has been reinforced by the experimental study of ecesis and competition in different associations. As a corollary of this, shrinkage comes to be seen as a dynamic process, typical of the phases of desiccation so characteristic of western North America. It is evident that these brought about such migrations as that of the prairie climax into the forest and of desert scrub into grassland. However, such advances

were contingent upon climate throwing the balance in competition for water to the side of grasses and against trees, and this meant the slow destruction and consequent elimination of forest, through three fairly well-defined stages. The first was the dropping out of the more mesophytic species, the second a withdrawal from the finer soils of the general level with a high echard, leaving the more xeric species in valley, on mountain ridges or in sandy soils, and the third the death of older and weaker individuals under the increasing competition of the grasses, resulting in the production of savanna.

A fourth consequence was the dwarfing of the individual trees, producing a unique series of climatic indicators, such as those of Oklahoma in which the dwarf oak or "shinry" of the western sandhills persists as the rearguard of the fine climax forest of the Ozark Plateau, the stragglers between increasing in height and density toward the latter. Shrinkage under the same climatic pulsations has produced the more extensive oak savannas or "Cross Timbers" of Texas in the long sandy inclusions of the "black-land" prairies (Plate 51B).

Utilization and Interpretation.—At the outset extensive and repeated survey is essential to disclose the largest possible number of relict communities of any particular type. This is important not merely to determine the area concerned, but especially also to reveal the degree of harmony between the various examples. Disagreement between some of these is often a source of new leads and frequently demands re-examination during other seasons and years. In most cases, such disagreement is merely superficial and disappears in the more thorough analysis afforded by comparison. It is clear that harmony can be expected only between relicts of the same type and due to the same cause, though in any particular climax there will be a certain degree of relation between relicts of different types.

Interpretation is a comparatively simple procedure, which deals in each instance with the cause as the clue to what has transpired in the past and may be expected in the future. However, it takes quite a different course in the case of climatic relicts than in those produced by the coactions of man and animals. In the former, it is based upon the clisere or series of climaxes that reflect increasing altitude and latitude on mountain chains or on continents. This is the sequence of communities that is moved back and forth by the phases of a major cycle, leaving relicts in all situations that possess proper compensation against the new

climate. In the case of the great coactions, such as fire, clearing and grazing, the process itself supplies the key to unlock the meaning of relicts, but the actual analysis must reckon with response to the changed factors, with reaction upon the habitat and the competitive equipment of the species concerned. Such analysis in typical instances is discussed with some detail in a succeeding section.

Since the clisere indicates the basic climatic relation of climaxes, it provides the most illuminating interpretation of such relicts. The bond between the included climaxes is well expressed in the statement that these move concomitantly with the shift of climate and that each bears a reciprocal ecological and topographical relation to the other. These inter-relations have been crystallized in the terms preclimax and post-climax (1916, 1928, 1929). In the static clisere of a great cordillera, such as the Rocky Mountains, the preclimax of the montane forest is the xeric mixed prairie at the base, and the postclimax, the more mesic sub-alpine forest at the higher altitudes. In periods of mass migration, the prairie is preclimax to the forest and the latter postclimax to the prairie, a relation discoverable at any time in the ecotone between them. Arctic tundra is preclimax to boreal forest, alpine tundra to subalpine forest; grassland is preclimax to scrub and forest formations, while these are typically postclimax to it. The same general principle holds for the associations of a formation, mixed prairie being preclimax to true prairie, this postclimax to the former; maple-beech is postclimax to oak-hickory, and the reverse, while hemlock is postclimax to maple-beech.

The term subclimax has been purposely employed for two some-what different concepts since its first proposal in 1916 to permit economy of terms until the need for closer definition became more generally recog-nized. A recent discussion of this matter by Godwin and by Tansley indicates that such may now be the case, and in consequence it is pro-posed to restrict subclimax to an actual subfinal stage in the sere. For those cases in which the community is modified and held for a more or less indefinite period in some other condition, as with the short grass plains of North America, the term "proclimax" is suggested. Since grazing, clearing and fire regularly exert a selective action, the majority of the communities heretofore called subclimaxes will now become pro-climaxes. However, it must be admitted that our present knowledge of development will not always permit an exact distinction between

the two, and furthermore that proclimaxes are not all identical in character (Plates 37 and 38).

Supporting Evidence.—It is obvious that interpretation on the basis of observation gains much from other methods when these are applicable. The primary canon of ecology is synthesis, in accordance with which it is imperative to utilize all the sources of supporting evidence. Though of various kinds, these may be comprised in four main categories, namely, (1) relations still existing in the climax, (2) records, (3) cycles as natural experiments, (4) experiment, especially in the form of closures. Constant attention has been paid to all of these during the period of relict studies and a large amount of material has been accumulated, the bulk of which must be left for detailed consideration in the future. Here it must suffice to suggest the methods and to assign to each its proper place in the synthetic pattern.

Although such great climaxes of North America as the deciduous forest and the prairie have been profoundly modified and fragmented over most of their respective regions, there are still areas in which the original relations of the dominants obtain, especially in the grassland. By using these as a standard for comparison, practically all degrees of change may be evaluated objectively and the task of interpretation greatly facilitated. During the period of these investigations, such correlations have been frequently established with relicts that were later destroyed, thus producing conditions identical with those in which relicts had disappeared too early for record and imparting to the course of events a certainty otherwise impossible of attainment. Of much the same nature and importance is the effect of annuation in response to changing phases of cycles. Wet seasons on the Great Plains, by increasing water content and decreasing competition, have regularly reproduced in convincing fashion the mixed prairie in wide stretches that are apparently short grass climax during dry years. In the Southwest, such periods have restored the grass dominants to a degree that leaves little for experiment in demonstrating that the *Larrea* community really constitutes a savanna in the desert-plains grassland (Plate 47A).

In the field of human documents, there are three chief categories to be considered, though these grade more or less into each other, namely: (1) scientific records, (2) exploring and surveying records, and (3) records and recollections of pioneers. The latter may be dismissed more or less completely at the outset, since they only have value in the excep-

tional cases where the settler possessed definite botanical knowledge. The same treatment applies to the boyhood recollections of naturalists and botanists, the most illuminating instance being that of a writer who speaks of being "intimately acquainted with the prairies since the year 1871," at which time he was five years old. The weight to be assigned records of exploration depends upon whether the personnel contained botanists or men with some technical knowledge of the plants, the myth of the "Great American Desert" being largely a tribute to the powers of observation of the layman. In forested regions, the logs of surveyors often possess values in detail, as Sears and others have shown. Finally, the records of scientists are naturally of the first importance, those of Bessey and his students in Nebraska and of the United States Division of Agrostology in the West generally, made from 1885 to 1900, being a mine of information for tracing changes in grassland.

After all the evidence indicated has been secured, the last element of certainty must be contributed by experiment. This is fairly simple in the case of grassland, more difficult with scrub and still more so with forest. The effect of fencing upon conservation and especially in promoting recovery was noted as soon as attention was turned to the theme of relict communities, and led logically to the extensive installations of exclosures and enclosures in Arizona in 1918. These and others in various associations have not only furnished decisive demonstration of the relation of relict to climax, but also revealed the role of stock and rodents in the process of modification (Plates 32 and 63).

The influence of climatic cycles in terms of annual variations in density and volume is measured by means of isolation transects, consisting of central strips permanently protected against cattle and against cattle and rodents, units being exclosed and enclosed each year to furnish a graduated annual scale of effects. In addition, series of small plots a few meters in area are installed to determine the effect of various processes, such as denuding, burning, clipping, sowing, planting, removal of grasses or forbs to measure competition, and so forth. Experimental exclosures of various types have been established for a decade or more in all the grassland associations and have confirmed the original field interpretations in every case (1929).

Kinds of Relict Communities

As indicated previously, relict communities fall into two well-defined major groups, viz. those due to climatic pulsations and those produced by

human coactions. Relicts of the first type owe their persistence to some compensating action of topography or soil, typically upon the holard, while the second type derives from protection in some form, usually as fencing. In a few cases, the same feature will exert both effects; thus a rocky slope or ridge will afford refuge to trees or shrubs by virtue of reduced competition and, at the same time, by reason of its steepness and uncertain footing protect grasses from overgrazing.

The variety of relict areas is so great that it is impossible within the limits of this discussion to give detailed treatment to all of them. In consequence, they are here passed in review with a brief mention of their salient features, while a few of the most important types are given more extended treatment.

Climatic Relicts.—By far the greater majority of these are due to the compensation afforded by topographic features, such as altitude, slope exposure, ridges, or valleys. The compensation provided by altitude operates chiefly upon water content through increased rainfall and decreased temperature, but it bears also a more or less definite relation to evaporation and transpiration. However, the difference in altitude must be neither too small nor too great; in the one case, it is insufficient to produce perceptible effects, and in the other it leads to the presence of a distinct climax. Elevation in terms of land-forms is expressed in hill, ridge and mountain, characterized by striking differences in exposure to insolation, due partly to period of reception, partly to angle of slope, and partly also to shadow. The effective difference between northerly and southerly exposures is again one of holard and transpiration primarily, with certain secondary effects of temperature.

The cooler moister slopes have been termed mesoclines, and the warmer drier ones, xeroclines, between which lie areas of smaller differences. The mesocline is regularly postclimax to the level plain, and the xerocline preclimax to it, while they bear a somewhat similar relation to each other. In periods of desiccation, the mesic communities shrink to the point of disappearance, first on the southwest, then south and finally southeast, usually making their last stand on northeast slopes; during wet intervals, the mesocline spreads to the southeast and south, but rarely invades the southwest slope. This relation holds true for all three major climaxes, forest, scrub and grassland, but naturally attains the most striking expression where two of these are concerned. In addition to the major features are innumerable finer details of value and interest, the presence

or composition of consociation or society shifting with small variations in angle of slope, exposure, surface, texture, or soil profile.

The seration, or sequence of communities across valleys, exhibits similar though inverted relations in comparison with the ecocline, by virtue of its concave form. The movement of run-off into the center of the valley, as well as cold-air drainage, determines this as the area of compensation, which is usually emphasized by the presence of a stream. Consequently, shrinkage proceeds from the walls inward, the characteristic fringing forests of prairie valleys being postclimax to the surrounding grassland. The walls or bluffs themselves present conditions closely resembling the two ecoclines of a hill, but the south wall has a north slope exposure and hence is a mesocline, while the northerly one with southern insolation is the xerocline. As with ridge and mountain, the valley exhibits minor relief in terms of breaks, ravines, vales, knolls, etc., with corresponding variation in the composition and persistence of relicts.

The understanding of climaxes and the interpretation of relicts is advanced by recognition of the fact that the clisere of a major mountain range, the ecoclines of a hill or peak and the series of communities across a valley bear much the same relation to climatic cycles. There is the same essential bond between the climaxes or climax relicts in terms of potential movement or of succession, of expansion and contraction, whether this be up and down the mountain slope, around a hill, or back and forth across a valley. By the careful comparison of all three in a particular region, it is possible to secure a long look backward into the past and forward into the future of the biome.

Probably the most dramatic, as certainly heretofore the most puzzling, compensation for desiccation has been that afforded by sandhills and sand plains. This is because the compensating factor, the soil texture, is not at once visible and the correlation of the great relict communities with a definite cause is far from evident. Such relations are to be found in sand or gravel soils everywhere, especially in ecotones, but the most striking and best-known cases are probably those of the sandhills of Nebraska and of the sand plains and river dunes of Texas and Oklahoma. The former are characterized by a tall grass postclimax in the midst of climatic mixed prairie, and the latter by extensive relicts of the former oak-hickory association that has shrunken into areas enclosed by coastal or by true prairie on "black-land." The preservation of the original climax in the form of a postclimax is due in both cases to the same type of com-

pensation, namely, the higher echard of sand by contrast with loam and the effect of the sand upon absorption and run-off. However, in the course of centuries or millennia, this advantage is gradually lost by the decay of organic material, the sand becomes finer and the echard rises, with the result that the forest first becomes savanna and is then more and more open, to the point of disappearance in the grassland. In the reciprocal climatic phase, the forest would encroach upon the grassland of the fine soils owing to the rise of the holard in conformity with increasing rainfall but the spiral-cyclic movement toward desiccation in North America since the Cretaceous permits few if any relicts of this type, at least outside regions of major glaciation.

As suggested earlier, the series of forest relicts extending through three prairie associations from New Mexico to Missouri affords a remarkable opportunity for their correlation—one perhaps unparalleled anywhere in the world. The westernmost relict is one of *Quercus muhlenbergi* in a deep canyon of the Capitan Mountains in New Mexico. On the sandy plains of eastern New Mexico and western Oklahoma, *Q. stellata* and other oaks are represented in the dwarf "shinry," at the extreme only a food high. Caddo Canyon and other deep narrow gorges of central-western Oklahoma still harbor relict forests of deciduous trees, in which *Acer saccharum* may be the chief dominant. Further east, oak-hickory relicts fringe the streams and persist as savanna on the ridges. Along the eastern border of the state, the massive outliers of the Ozark Plateau are covered with dense savanna of tall trees, and on the Plateau itself this passes into oak-hickory climax, with postclimax maple in the deeper valleys and rarer relicts of beech.

Relicts Due to Human Coactions.—While these are all a consequence of the operations of man, his action is an indirect one in the case of grazing especially. In practically all cases, the compensating factor is protection, though this assumes quite different forms, from such physical barriers as fences at one end to moral or legal restraints at the other. Obviously, the overwhelming number of coaction relicts are the result of fencing, and the others serve chiefly to attest the principle. Quite as clearly, it is "fencing-out" or exclosure that counts in the conservation of relicts, since overstocking and consequent overgrazing of fenced pastures and ranges have caused universal modification of the original climax (Plates 32 and 63).

In actual practice, fencing bears no such relation to forest as it does

to grassland. The general effect of clearing and lumbering has been to destroy the forest, to the extent that relicts persisted only in inaccessible regions or in tracts of little or no economic importance. On the other hand, fire, intentional or otherwise, has known no restraint until the era of conservation, with the consequence that untouched forests are all but unknown between boreal and tropical regions. However, the sprouting faculty of deciduous trees has counterbalanced lumbering and fire in large measure, and extensive relicts in the form of "second-growth" are to be found throughout the deciduous climax. In the case of some conifers, the general absence of sprouting has been offset by the resistance of thick bárk as in *Pinus ponderosa,* or the peculiar equipment of the seedling as in *P. palustris,* and even more by the vagaries of wind, weather, or terrain in modifying the course of fires and leaving relicts. As in other respects, scrub falls in between grassland and forest, inasmuch as it readily forms root sprouts, with a few notable exceptions like sagebrush, but often requires protection from browsing.

Because of their frequence, continuity and the relatively early date at which they were fenced, railroad rights-of-way surpass every other source of relicts in the Middle West and Far West. For much the same reasons, roadways come next in importance, though the fencing of the adjacent fields and pastures is less regular and often more recent. Both present a myriad of relicts under the whole range of climax conditions and structures and for this reason in particular their analysis is carried out in some detail. Fencing in other forms likewise leads to the preservation of relicts, as in the corners of fields, between fence and field-edge, in cemeteries, rural schoolyards, many farmyards, and so forth. An indirect effect of fencing is seen in the immunity of hay lands from grazing, and this often extends also to unfenced roads and railways. A similar consequence occurs in the twilight zone between town and country, where in grazing regions some of the best relicts are to be found by virtue of custom or actual regulation (Plate 43B). Vacant lots in cities frequently exhibit areas of the original grassland practically unchanged, and some relicts of this type are known to be fifty to a hundred years old.

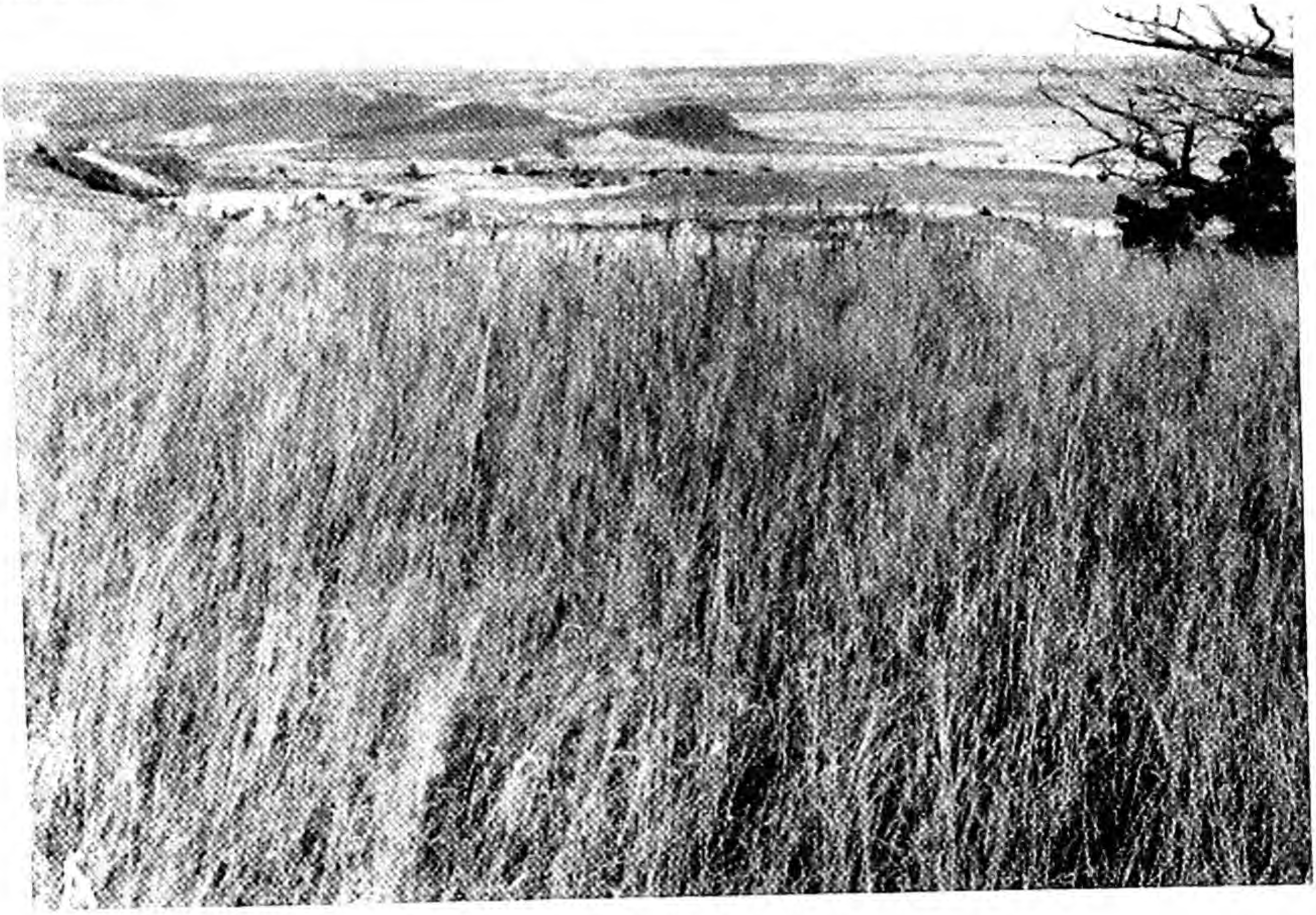
In the case of reservations and reserves set aside by law, the areas are generally the most extensive of all, but their value as relicts is determined in large measure by their age and type of utilization. The Indian reservations are the oldest of these and they afford unsurpassed examples of climax grassland when leasing has not permitted overgrazing. National

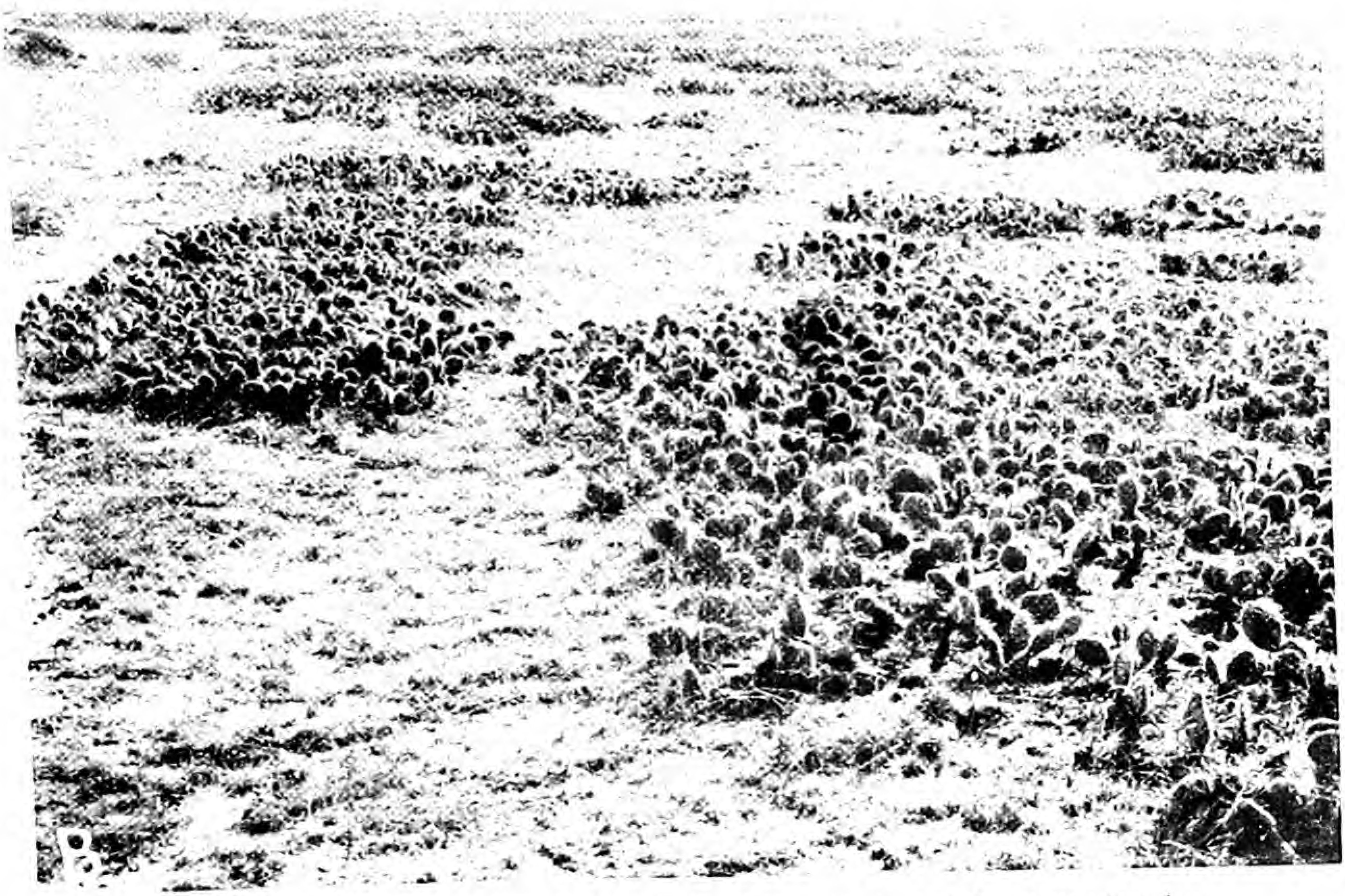
parks and national forests are usully of later date, but intelligent conservation in both and the actual regeneration of the range in the latter give great and growing value to these as sources of relicts. Most valuable of all, however, are sach grazing ranges as the Santa Rita Reserve in Arizona, the Jornada in New Mexico, and the Wichita in Oklahoma, in which use under proper regulation is supplemented by exclosure and other experiments. In the case of game preserves and refuges, and state parks, relict values are sometimes secured, but too often the lack of regulation and the kind of popular utilization have no effect other than to render them object lessons.

Other types of protection that produce relict communities are an outcome of barriers of various sorts. Precipitous slopes and abrupt canyons prevent the access of stock more or less completely, as in the classic example of Sheep Mountain and Medicine Butte (Plate 44A) and this effect is sometimes produced by swift streams. A district without surface water rarely permits utilization of the grass, and such areas are today practically unchanged by coaction. Even on a cattle range, distance to water determines the degree of grazing and the more remote portions are usually much less utilized. Finally, cacti, bushes with spines or thorns, or with dense stiff branches regularly serve to protect the grasses growing in or near them, sometimes providing the sole evidence of the former grassland over extensive areas (Plate 44B).

Some types of soil provide a certain amount of compensation for coactions, in something of the manner they do for climatic changes. Sand, by virtue of its large amount of available water, regularly affords a refuge from overgrazing, to the extent that the plants grow more vigorously, especially in dry seasons, and the competition for water is less than in hard soils. A pebbly or flaky soil has something of the same effect, though the reduced cover is the chief feature in maintaining a better water content. A rocky terrain also offers handicaps to a good footing, as well as to actual grazing, especially when the rocks are upthrust in ridges, and the ecologist in search of relict grasses and forbs rarely inspects such an area in vain.

The Trackway as a Relict Complex.—The value of a right-of-way as a relict area depends primarily upon its age and upon fencing. The latter has significant effects only in the grassland climax, or rarely in scrub. The fence must have been installed at the time of construction or at least not so long after as to permit serious modification, and must have



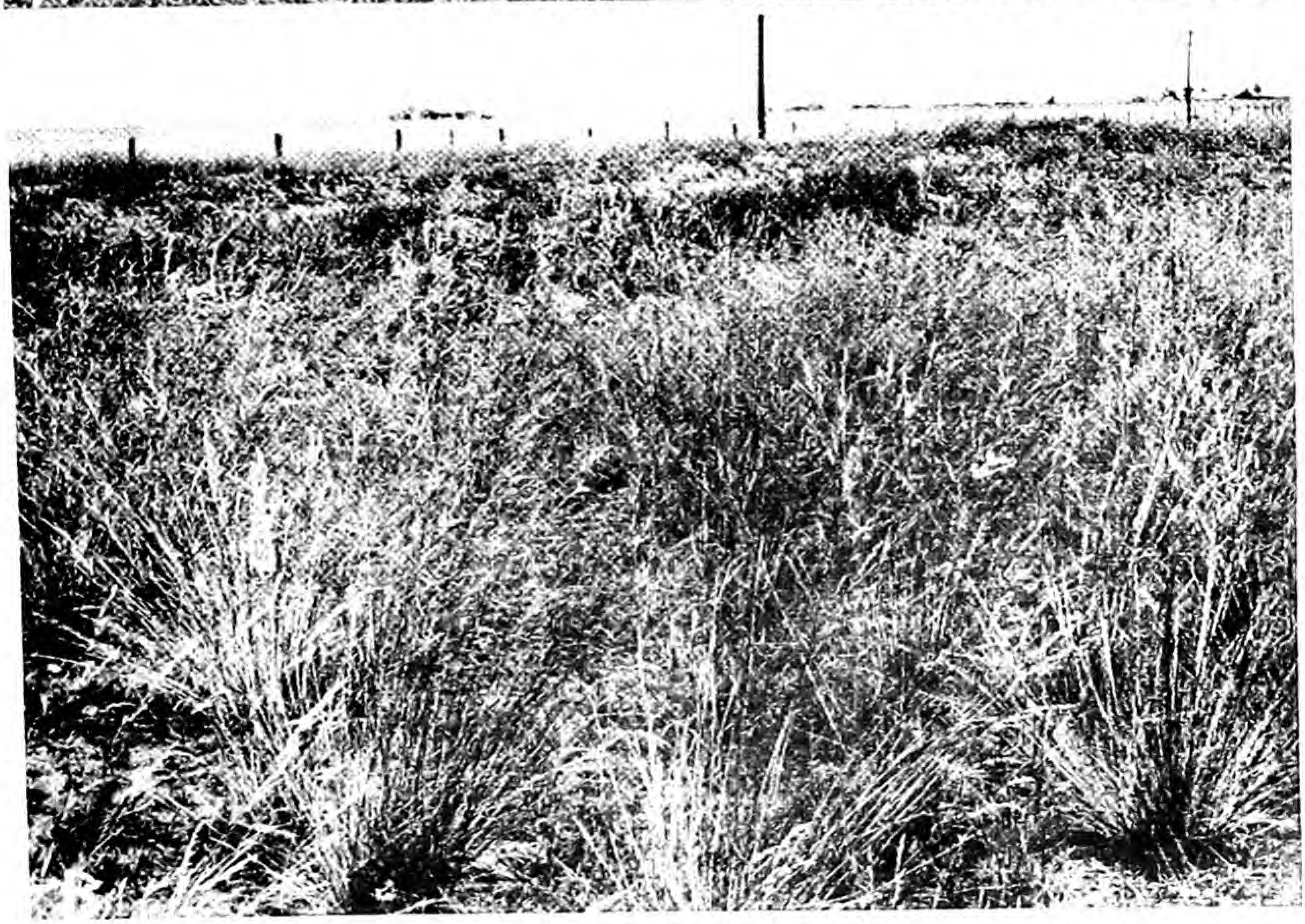


A. Mixed prairie on top of Medicine Butte, protected from grazing by precipitous walls, South Dakota.
B. Relict grasses protected by *Opuntia* in overgrazed pasture, Great Plains, Colorado.

been well maintained. Trackways without fences or with these broken or later removed are not to be ignored, but the evidence obtained from them must be scanned in the light of fenced railways in the same district. In the case of those long established in populous regions disturbances of all sorts have occurred to replace the natural grassland with ruderals, while railroads of recent construction are usually laid down in a cover already much modified.

More and more are rights-of-way mown and even grazed, burned each year, or used for cropping, as was especially the case during the war period of 1917-18. In addition, the cover has been much changed in consequence of the disturbance resulting from construction, in the form of road bed, cuts, fills, dumps, and ditches. As a result, nearly every trackway is a mosaic of climax and seral communities, especially of the subsere. The distinction between these is rarely attended with doubt when made on the basis of indicators alone, but this can always be confirmed by the nature of the terrain itself. Through rolling prairie and sandhills, the trackway is an endless succession of serations, of swale or valley, level, and hillock or hill; the vales are regularly postclimax or seral in character, the levels climax for the most part, as are the hills also except when they are low enough to permit the dumping of material on the tops. On plains the climax was formerly continuous for the most part, but this has sometimes been modified over long distances by severe burning and not infrequently by ploughing (Plate 45A).

Transversely, a trackway consists of two sets of parallel zones, one on each side of the road bed. These both change from lowland to level and to hillock depending upon the manner and degree of removing the soil, and they sometimes differ from each other when bordered by a road or by different kinds of cultural and native vegetation. The road bed, where built up, is the site of weedy subseres in all stages unless it is ballasted or oiled, though the weeds are often cut or burned each year. When the bed lies on a high fill, the slopes of the latter permit the development of larger ruderal associes and these often lead to some phase of climax or subclimax, when the trench at the base is not too deep and wet. If the latter is broad and shallow, it is the site of postclimax species, for example tall grasses in both true and mixed prairie, and differs little from the postclimax vales. This ditch is usually excavated from the climax level, which is typically covered with the original grassland, with allowances for the various disturbances already mentioned. At the fence line, the



A. Tall grass community of *Andropogon furcatus* between roadway and trackway, Urbana, Illinois.

B. *Stipa pulchra* consociation of San Joaquin Valley as seen in a trackway near Fresno, California.

level is often modified by the invasion of ruderals from roadside or field, or by the cropping of stray horses or cattle. In the case of cuts, both the road bed and slopes are poorly colonized, unless the latter are sufficiently oblique to permit invasion from above. When the excavated dirt is piled on the original hillock, a short ruderal subsere ensues, soon followed by invaders from the climax, and this is sooner or later reconstituted. Cuts are often protected by snow breaks that by virtue of drifting snow and summer shading bring about certain changes, but usually well within the climax range.

The Roadway as a Relict Complex.—As a result of greater variety of type, roadways often furnish a wider range of evidence than trackways, though the relict areas are smaller and less continuous, owing to constant disturbance and readier invasion. The relict strip between road bed and fence is rapidly being eliminated along main motor highways, especially by successive widening, but it will persist for a long time on secondary ones and still longer on country roads and trails. Roadways naturally resemble trackways in the seration features of valley, level and hill and increasingly so in the provision of deeper cuts and fills; they are likewise characterized by parallel strips on either side of the bed.

Except on surfaced roads, the roadside is usually occupied by decumbent ruderals held in an initial stage of the subsere by packing. This slopes gently to a ditch often flooded and hence occupied more or less permanently by tall annuals and perennials. Above this rises vertically the road shelf, which is regularly little affected by road making and bears a more or less continuous cover of relicts. These may extend into the field strip inside the usual barbed wire fence, may lose themselves in the modified cover of pasture or range, or continue into schoolyard, farmyard or cemetery. The wire fence rarely exerts any distinct effect upon the relicts, but rail and board fences and hedges frequently conserve relicts by reducing evaporation and transpiration and increasing the holard through foliage drip.

Since road shelf and field strip are protected from all but sporadic grazing, the persistence of relicts in them is largely determined by the invasion of ruderals and the consequent competition. Both field and experimental evidence demonstrate that weeds quickly yield to native grasses when invasions are single or infrequent, but the recurrent and increasing pressure of weeds finally causes the disappearance of grass. The outcome is chiefly determined by the ease with which the seeds of

weeds reach the relict areas. When the shelf is low and the adjacent field weedy, invasion and competition are at a premium and the strip becomes dominated by a short and persistent subsere. If the shelf is high, the chances of the relicts are greatly improved, especially in front of a pasture rather than a tilled field. The shelves of deep cuts are best protected from invasion from the road and, since such country is generally used for grazing rather than crops, almost equally well from the other side. In consequence, the shelves of such cuts are standard refuges for relict grasses, especially in California where they have been crowded out in all the lower intervals by the introduced annual grasses.

From such shelves, grasses and forbs, especially *Stipa,* colonize the slopes, and this has sometimes given rise to the erroneous impression that *Stipa* has "come in" from some vague source. However, in practically all such cases, the original climax group still persists above, to leave no doubt of the actual process. When a road shelf a few feet high is paralleled by the ditch, as is regularly the case, the edge is often marked by a taller and denser growth of grass relicts; this is due partly to reduced competition at the ditch. Such edges and ditches also serve as easy pathways for alternating migration and ecesis of tall grasses from the lowlands, and thus explain in part the gradual encroachment of these upon the mid grasses of slope and upland in both true and mixed prairie.

From the preceding, it becomes evident that trackways and roadways furnish an amount and variety of evidence as to the course of modification and manner of control of grassland that cannot be matched elsewhere. No adequate and accurate understanding of the climax is possible without taking these into account; as a field procedure they warrant more attention than is given other relicts because they permit the ecologist to use interpretation with a certainty and detail otherwise impossible. For this reason it is desirable, especially in prairie regions, that the trackways be first examined before proceeding to the inspection of pasture or open range (Plate 45B).

Application of the Relict Method

In applying the relict method to the interpretation of a particular climax, it is important to realize at the outset that the structure of the latter is a mosaic of climatic, seral, and coactive effects. The initial task is to distinguish these on the basis of both cause and process and thus

disclose their interrelations. This is a fairly simple matter in the case of priseres and subseres, since the sequence of stages is more or less evident, but it demands a wider survey extending through several years to recognize the various climatic indicators. When these consist of a typical portion of the association or of its subdivision, the faciation, the nature and relationship of the relict are usually evident, but this is less true of the consociation, consisting of a single dominant. However, in such cases, the clue is furnished by the rule that dominants, like associations, arrange themselves in more or less definite sequence, the reciprocal relation between them being maintained under practically all changes of climate. The test of this is afforded by the plus and minus phases of the climatic cycle, and hence the study of the responses of both climax and relict to such extremes is indispensable to proper interpretation. In western North America, the amount of rainfall at the sunspot minimum may be three to four times greater than at the maximum, and the potential changes of the climax may approximate those of a major climatic pulsation.

Coaction is so widespread and recurrent that its major consequences are often readily recognized. However, in the case of relicts, the process may be no longer in effect, its operation may be obscure, or it may be complicated by the concomitant action of other processes. In consequence, it becomes necessary to read the evidence in the light of each type of coaction in actual operation, and finally to appeal to experiment for a conclusive judgment. While fire and lumbering, for example, have very obvious effects, these relate chiefly to destruction, and the detailed course of the coaction is but little understood. This applies with especial force to coactions in grassland and in scrub, where the procedure is more obscure or at least less conspicuous. The selective action of burning is probably decisive in the large majority of cases, and mowing, generally regarded as of little or no influence, usually produces a distinct and sometimes a pronounced effect. Hence, in the interpretation of relicts, a synthetic approach in the light of all the evidence, supporting as well as indicator, negative as well as positive, is imperative if objective values are to be secured.

Interpretation in the Grassland Climax.—The value of the relict method for interpreting the present structure of the grassland climax and retracing the changes concerned may be illustrated by three outstanding problems in it. These are the origin and significance of the short grass proclimax, the original dominants of the California prairies, now gener-

ally replaced by annual grasses, and the invasion of bluestem and bluegrass into the eastern true prairie, at the expense of the midgrass dominants. Before this method was called into requisition, it was inevitable that the community in possession should be regarded as climax, except in California where the native forerunners of the annuals were unknown. This was the view embodied in the *Phytogeography of Nebraska* (1898) and generally adopted for two decades, until comparative studies of the several grassland associations in the light of climatic cycles and human coactions led to its modification (1920).

Short Grass Proclimaxes.—By far the most extensive and best known of these is the short grass community of the Great Plains, stretching through the mixed prairie from Saskatchewan to Texas. However, the essential relations for the production of such a proclimax exist wherever short and tall grasses occur together and are subjected to overgrazing. This is notably the case with matformers such as *Buchloe dactyloides*, *Hilaria cenchroides* and *Cynodon;* together with several species of *Bouteloua* one or more of these regularly replace mid grasses and tall grasses in true, coastal and subclimax prairie under intensive grazing in pastures (Plate 26B).

The first intimation that the short grass plains were not a climax in the climatic sense was obtained during the summer of 1915; this was a season of excessive rainfall coinciding with the lowest sunspot minimum known for a century. The mid grasses appeared abundantly in the cover of short grass and in many places obscured the latter more or less completely. Since these were all perennials, it was obvious that they could not be regarded as recent invaders but must have been present in the community in less conspicuous form. This led to a search for protected areas in which they retained much of their normal importance and resulted in finding such relicts in a wide variety of situations. The protection afforded against grazing by fences usually supplied the most striking examples, as in the case of trackways, reserves and cemeteries especially, but sandy soil and rocky slopes regularly yielded mid grass dominants. This explanation was supported by the course of events leading up to the drouth period of 1917-18, when the taller grasses diminished in height, failed to produce flower-stalks and became relatively inconspicuous in the dense short grass sod. A similar fluctuation was found in succeeding cycles of dry and wet years without exception, and this effect can now be traced in the accounts of various expeditions, the dis-

cordant opinions of the "Great American Desert" being readily harmonized on the basis of the sunspot cycle in relation to rainfall.

During the intervening period, many thousand relicts of all sorts have been recorded throughout the mixed prairie, and their significance has been confirmed by an increasing number of experimental exclosures, in all of which protection against grazing has enabled the mid grasses to regain their normal dominance. In a few areas, especially on soils with the highest echard, overgrazing has led to the practical disappearance of the mid grasses, but in none of these are the latter absent from protected spots in the vicinity.

Bunch Grass Prairie of California.—The valleys and hills of California are today covered with a continuous mantle composed of annual species of *Avena, Bromus* and *Festuca.* These have seemingly replaced the native perennials, *Stipa, Poa, Koeleria, Melica,* etc., so completely as to have produced grave doubt as to the composition of the original climax. In a country with winter rainfall, the perennial grasses are especially susceptible to damage by overgrazing during the annual dry period from May to December, and the outcome of 150 years of grazing and cropping has been to establish the wild oats as the one great dominant throughout. Because of its height and vigor it has been conserved for hay over large stretches and, since it also withstands grazing fairly well, it has come to simulate a climax in many respects. However, in recent decades, it has suffered more and more from overgrazing and is gradually being replaced by bromes, fescues and barleys (Plate 30C).

The search for bunch grass relicts in 1917-18 was first directed to trackways, not merely because such relicts were often remarkable in purity and extent, but also because they were rapidly being destroyed as a war-time measure to produce a great crop of wheat. Many hundred miles of a nearly continuous consociation of *Stipa pulchra* were obliterated in the Great Valley, leaving sparse fragments where plough and fire had taken lighter toll (Plate 45B). It was especial good fortune to record these extensive relicts and then to have seen them reduced to patches here and there, as it not only confirms the other evidence to the effect that grassland was the original great climax of California, but it also throws needed light upon other regions known only by the mosaic of relicts.

The transformation of southeastern California from bunch grass prairie to desert as a consequence of climatic changes is attested by a

variety of relicts in Death Valley, the Mohave, Colorado and Sonora deserts. For the most part these occur sparsely, a fact explained by the range of rainfall from 1 to 5 in., and are found chiefly on the mesoclines of the lower mountains and at altitudes of 3-5000 ft. in the higher ones. Sand and lava fields have formed a refuge for several of the most xeric species, while the most typical of all, the shrubby grass, *Hilaria rigida*, seems to have been derived directly from the adaptation of *H. jamesi* to a drying climate. Now a dominant of the southwestern faciation of the mixed prairie, the earlier extension of the latter species over the desert region is proved by relicts in the mountain borders. This assumption as to the origin of *H. rigida* is further supported by its regular preference for sandy plains and washes with a higher water content (Plate 43A).

True Prairie.—The key to the understanding of this climax association is to be sought in the place of origin and the life history of its dominants. Of the climax dominants, *Koeleria* and *Agropyrum* are circumpolar, while *Stipa spartea* is boreal, and *Bouteloua racemosa* southwestern. *Andropogon scoparius* ranges well to both north and south, but it is southern in origin, while *Sporobolus asper* and *S. heterolepis* are essentially southern. The postclimax dominants of low prairie, *Andropogon furcatus* and *Sorghastrum nutans* are widespread but of distinctly southern derivation, while *Panicum virgatum* is still more austral and *Elymus canadensis* northern. The preclimax *Boutelouas* and *Buchloe dactyloides* stretch to the Canadian border or beyond, but their original home is far to the Southwest. The invading *Poa pratensis* is circumpolar, but the form in the true prairie has come from Europe by way of the East.

As a rule, the species of northern affiliation appear earliest in the spring and hence bear the heaviest brunt of grazing, as well as injury by spring fires. These are *Stipa spartea* and *Koeleria cristata* in particular; flowering occurs early likewise, in the central region during May. The preclimax short grasses reach the optimum in early summer, *Bouteloua racemosa* in mid-season, and the postclimax tall grasses in late summer, *Andropogon furcatus* and *Sorghastrum nutans* blooming in late August or early September. *Sporobolus asper* is much the latest of all the dominants, the panicles often not appearing until the end of September. As the name June-grass indicates, *Poa pratensis* forms its flower culms early, at a time to give *Stipa* and *Koeleria* the keenest competition. *Agropyrum* blooms in midsummer, while *Andropogon scoparious* may slightly precede its taller relatives.

In terms of the competitive equipment of shoot and root, *Andropogon furcatus* takes first rank, followed closely by *Sporobolus asper,* and this by *Sorghastrum nutans* and *A. scoparius.* In spite of its tenacious rhizome, *Agropyrum* is a weak competitor, and the short grasses maintain their place only by virtue of their xerocline proclivities. *Stipa* is fairly well equipped for holding its own, as is likewise *Bouteloua curtipendula* while *Koeleria* is rather less sturdy. However, the surprising competitor is the low and delicate *Poa,* but this owes its success chiefly to human coactions.

The basic relations of the dominants are clearly indicated in the three life forms, namely, tall, mid and short grass, and are reflected in the harmony seen in the edaphic and climatic correspondences of each group. The tall grasses occurred originally in the low prairie and still exhibit the best development there, as would be expected from their dominance in the subclimax prairie to the eastward. In other words, the tall grasses are postclimax in the true prairie. The short grasses are characteristic of ridges and xeroclines, in agreement with their climatic dominance in the more xeric mixed prairie to the west; they are in consequence preclimax. Finally, the seven mid grasses occupy the general prairie levels between lowland and ridges, and constitute the actual climatic dominants. However, in the true prairie today, *Andropogon furcatus* is often found well up the slopes of rolling hills and sometimes on hill tops; *Stipa* and *Koeleria* are often much reduced or lacking, *Sporobolus asper* is usually entirely invisible in relict hay fields, and *Poa* has become widespread in swales and on cooler slopes especially.

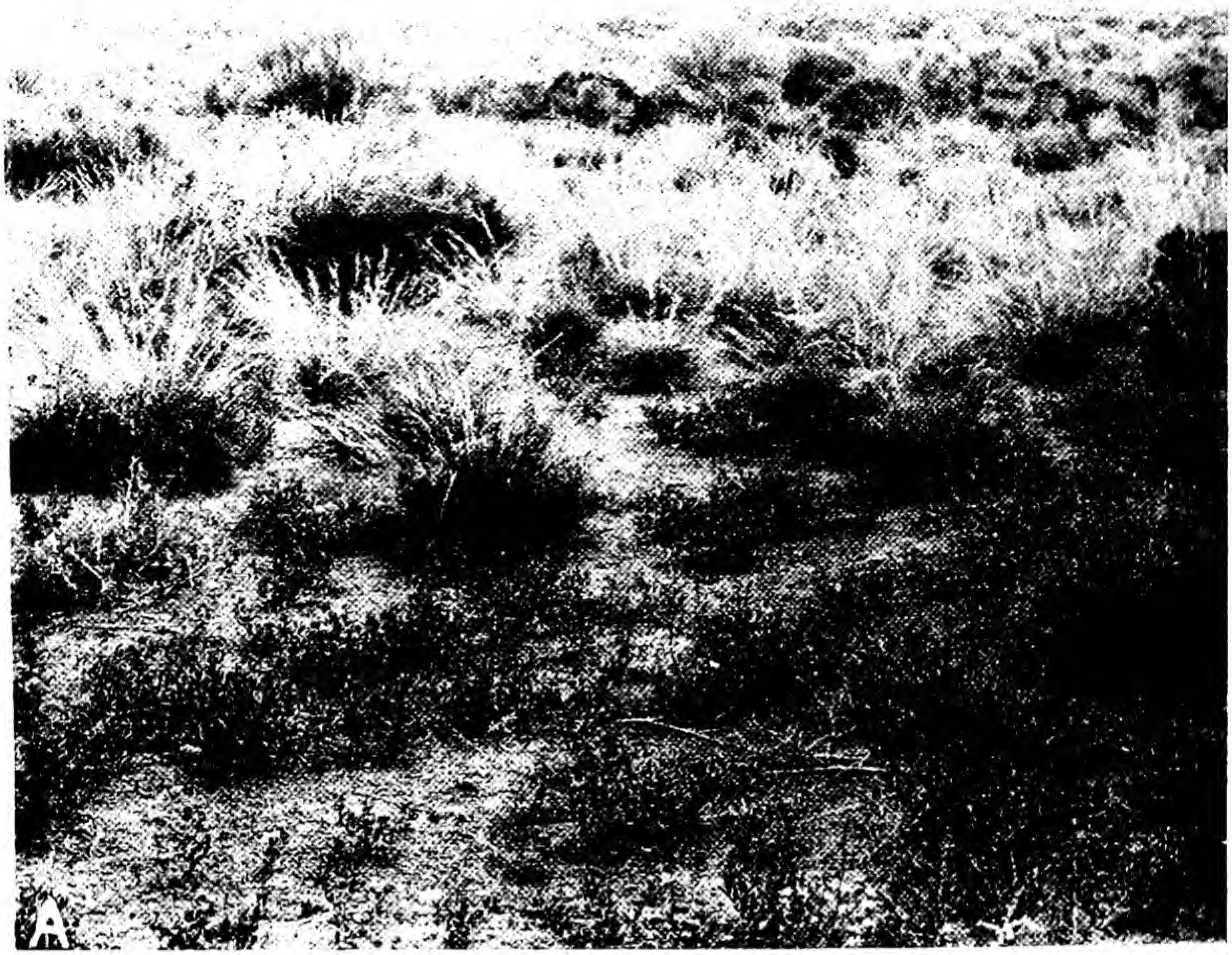
The detailed explanation of these changes and the consequent reconstruction of the original prairie are too long for the present purpose, but the main features may be indicated briefly. The processes involved in the coactions of grazing, fire, mowing, clearing and settlement generally have exerted a selective action upon the various dominants in accordance with life form and life history. As the first forage in spring after stock have been on dry feed for several months, *Stipa* and *Koeleria* have suffered much more severely than any other dominants. Moreover, this places them at a disadvantage in their competition with *Poa* and handicaps them both in the persistence of the adults and the production of seed. Early burning is also a feature in some districts. At the other end of the growing season, the tardy *Sporobolus asper* is hampered by the practice of mowing in late August, so that storage in the crowns is re-

duced and the formation of seed prevented. Likewise it suffers more from fires set in the autumn, but in spite of these handicaps, its vigorous rhizomes keep its place as well as those of *Andropogon furcatus*, and its disappearance in relict hay fields is usually apparent rather than real.

Fortunately, there is contemporaneous evidence of greater abundance previously for *Stipa* and *Koeleria* and of the upward march of the *Andropogons* in Kansas, Nebraska and South Dakota. Part of this is contained in herbaria and in lists and maps of distribution, supported in a general way by the widespread belief that the "bluestems followed the settler." More important still is the printed record for Nebraska (1898) and for South Dakota, as well as the journal of the Missouri and Niobrara grazing trip in 1893. In the forty years that have elapsed, the problem of changes in the true prairie has received continued attention, with the result that *Stipa*, for example, has been found in hundreds of relicts in Kansas, where it reaches its southern limit today. This is in spite of the fact that some observers say that they have never seen it in this state, presumably implying that it does not occur there.

Interpretation in Scrub Climaxes.—No other life form has raised so many difficulties of interpretation as the shrub. This is largely because of its size and visibility as contrasted with grasses, but partly also by reason of the ease with which it gives rise to savanna. At first thought, the latter conveys the impression of a climax, a view that needs to be corrected by careful consideration of the shrub as a climatic indicator, and especially by its peculiar relation to fire and browsing. While its life form indicates an intermediate position between tree and grass, this is true only in fairly humid regions; in arid ones, the typical shrubs are more xeric than grasses and hence become climax only in deserts. Another general misconception relates to the effect of fire, the perennial woody stems suggesting that scrub is injured more than grass by burning. This is true of a small number of shrubs, such as the sagebrush, *Artemisia tridentata*, which do not form root sprouts readily, but in the great majority of cases, fire increases the dominance of scrub at the expense of grass. When the latter is hampered by grazing, the disparity is even greater, and the effect of these combined coactions has everywhere been to develop scrub into a proclimax that masquerades as a true climax.

To permit this to happen, it is essential that shrubs be present upon which fire and grazing can operate. Such a situation was brought about by their northward migration in the wake of a climatic shift toward



A. Relict *Stipa* in sagebrush savanna, Hagerman, Idaho.
B. Relict *Agropyrum*, *Stipa*, etc., in cemetery, Huntington, Oregon.

desert; in the Southwest this might well have taken place at the time of the elevation of the Sierra Nevada during the Miocene. With the return of the grasses during an ensuing wet phase, the shrubs were enabled to hold their ground in favourable spots here and there, producing a very open savanna. It is probable that such stragglers increased slowly in number, especially during wet periods, but their great wave of abundance has undoubtedly been a consequence of man's coactions and chiefly during the historical period. This effect has been exerted upon three scrub communities of the Southwest, namely, sagebrush, desert scrub and mesquite, all of which exhibit similar savanna relations in grassland. The differences between them are primarily an expression of life form and life history in relation to fire, grazing, and migration devices.

The chief dominant of the sagebrush, *Artemisia tridentata,* occurs as the most conspicuous plant over a vast extent of territory, and this has naturally led to regarding all this as climax. The search for relict grasses disclosed their presence throughout the major portion of the area, indicating that it is in reality sagebrush savanna (Plate 46A). While sagebrush is browsed to a considerable degree, this is chiefly in the absence of a grass cover. Grass suffers much more severely under heavy pressure from stock, especially during drouth periods, and has been rapidly replaced by *Artemisia* and its associates over most of the area concerned. This conclusion is in harmony with the record of changes in the vegetation of the Great Basin since the period of settlement, and is now placed beyond question by the evidence drawn from experimental exclosures.

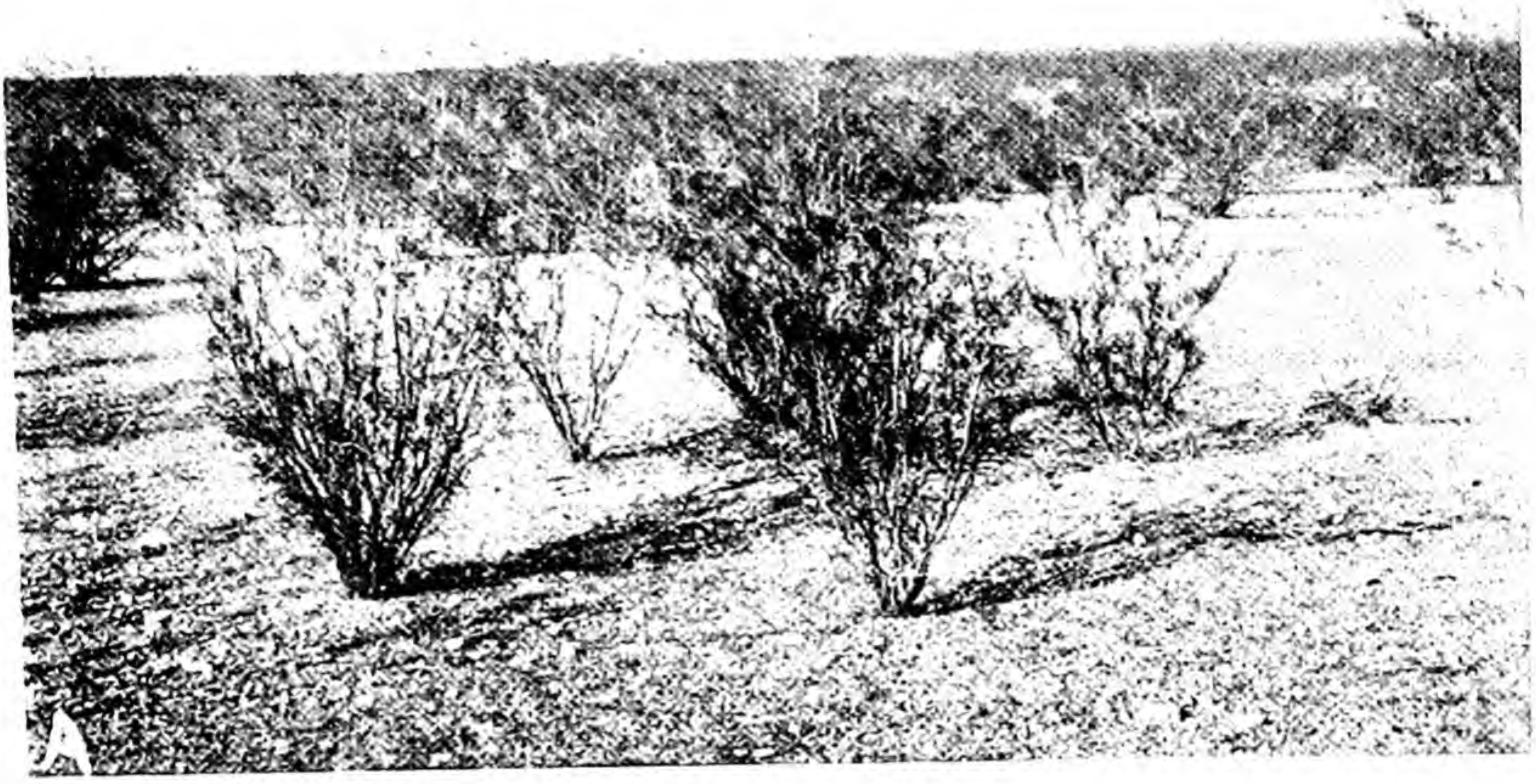
The region in which sagebrush might be mistaken for a climax today is little more than a fourth of the area over which this species appears to be dominant. This is the driest portion, in which the grasses have disappeared under the swing toward desiccation, yielding their places to the more xeric bushes. The wide movement of the latter during the historical period has been almost wholly a consequence of overgrazing of the grasses. Fire has not been much utilized by stockmen, since it tends to reduce the browse, owing to the reluctance of the species to produce root sprouts.

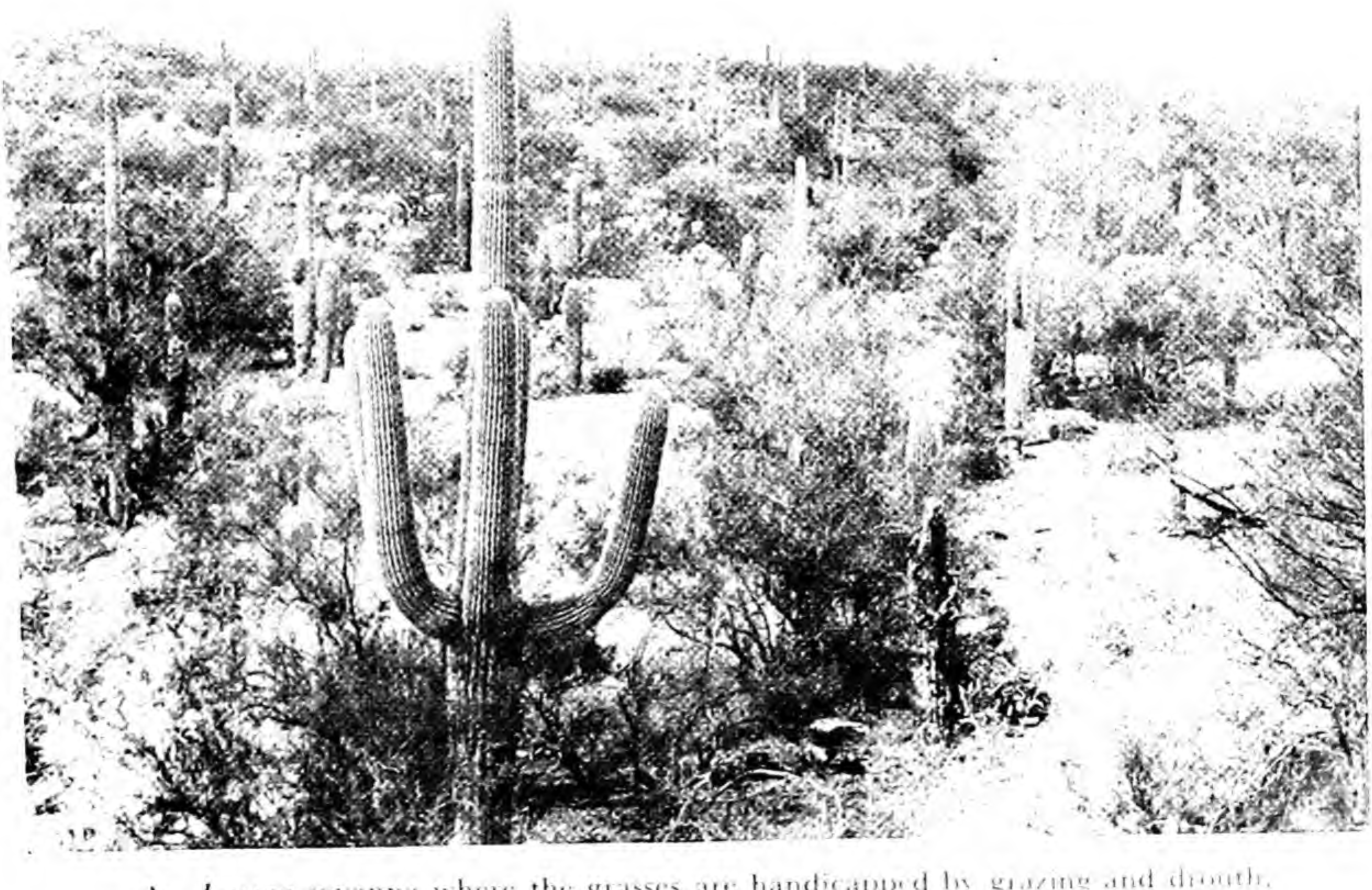
Desert–scrub Climax.—A broad band of *Larrea tridentata* sweeps from western Texas through southern New Mexico and Arizona and adjacent Mexico into the desert regions of transmontane California and lower Nevada and Utah. Like the sagebrush, it is the most dominant

note in the landscape, at the lower levels especially, and it is again understandable why it was mistaken for a climax community. Not only does it occupy a region early entered by man, but one also in which climate rendered grazing the major industry. In addition, it is a region in which drouth is frequent and widespread, with consequent handicaps to grasses under the impact of grazing. This resulted in upsetting the climatic balance to the advantage of the shrubs, an effect enhanced by the necessity of yearlong grazing. As an outcome of the combined influence of climate and overgrazing, the control of the shrubs had come to appear complete, resulting in the designation of "arboreal desert."

For the reasons just given, the application of the relict method was attended with more than the usual difficulty. However, the existence of fine grasslands at elevations of 3000 ft. and higher, coupled with the amount and type of rainfall, made the assumption of a grassland climate and climax probable. The quest for relicts was a more arduous one, but attended with much the usual success, differing chiefly in the smaller number and size of the areas. Probably the most striking examples were those found in old cemeteries, such as one in Huntington, Oregon, and another at Tombstone, Arizona, which afforded a detailed record of composition and structure in a district where perennial grasses are practically absent (Plate 46B). Sand and gravel areas were also fruitful, while mountain mesoclines and canyons at low altitudes yielded all the species to be found as dominants in the existing desert plains at 3-4000 ft. Most illuminating of all were extensive areas of dominant *Bouteloua, Aristida* and *Sporobolus* during wet phases in the outskirts of Tucson, where hay had been cut within a generation. This was further corroborated by the presence of desert-plains grassland little modified under the protection afforded by Indian reservations, through the entire period of settlement. A unique and invaluable background to the discovery and interpretation of grassland relicts was the presence of the Santa Rita Range Reserve and the fenced grounds of the Desert Laboratory at Tucson.

By the combined use of relict grasses as indicators and of isohyets, it has been possible to draw a broad line between the *Larrea* savanna, which is in reality desert-plains climax, and the desert proper. The latter consists essentially of two dominants, *Larrea tridentata* and *Franseria dumosa*, with many less abundant or locally important associates. In general, the ecotone between them is outlined by the isohyets of 5 and 6 in.





A. *Larrea* savanna where the grasses are handicapped by grazing and drouth, but persist as relicts; Arizona.

B. Postclimax of tall shrubs and small trees, with *Carnegiea* especially striking; outwash plain near Tucson, Arizona.

of rainfall. On the many broad outwash plains and the bajada slopes of the mountains are found postclimaxes of tall shrubs and small trees, among which *Carnegiea, Fouquiera* and *Yucca* are especially striking (Plate 47).

Mesquite Postclimax.—Throughout the *Larrea* savanna and the desert-scrub climax, *Prosopis* and *Acacia* are more or less typical of valleys and lowlands, constituting a fairly definite postclimax. Their water requirements explain why it is that in the higher rainfall of southern Texas they occupy the general level of the plain and give the appearance of a climax of low trees. In fact, the height and density of the individuals not infrequently justify such a conclusion, and a comprehensive analysis is required to disclose the real situation. Such a procedure was directed both to the behavior of the individual and to the climatic and competition relations of scrub and prairie.

Though its associates resemble it in varying degree, *Prosopis* is unsurpassed in successful migration and its powers of adaptation. Its sugary pods are eagerly sought by cattle, while the bony seeds are not affected by digestion and are voided under conditions especially favorable to germination. The leafy twigs are browsed to some extent, but the thorns prevent any serious damage from this source. Its powers of producing root sprouts are enormous and it is hardly possible for fire to be sufficiently frequent to kill it. Under the most adverse conditions it becomes decumbent in the form known as "running mesquite," in which it awaits the return of favorable circumstances. Its range of adjustment from such forms to trees of fair size give it a great advantage in competition with other woody plants and especially with grasses, so that it is regularly the chief dominant in the postclimax.

From the preceding, it becomes clear that the current assumption that fire favors grassland at the expense of mesquite is incorrect. In short, all the evidence demonstrates that instead of mesquite being eliminated by prairie fires, it has been decisively favored by them. Although the native grasses are not injured by fire as a rule, they derive no such advantage in competition as that secured by *Prosopis* from the increased number of shoots and density of individuals, particularly when dissemination by cattle is taken into account. As to the food coaction, mesquite is usually damaged little or not at all by browsing, while overgrazing may remove the grasses more or less completely, again giving the mesquite a decisive advantage in the competition. Taken in combination, these

features readily explain the great extent of mesquite and its ability to simulate the role of a climax dominant.

The repeated examination of the mesquite postclimax over a large part of its range discloses the general presence of grass relicts, except where grazing has been most severe, resulting in the production of "motts" or groves with a fairly close canopy. The usual condition is that of a more or less open savanna, in which the composition and density of the grass cover vary with the degree of grazing. In the absence of overgrazing and frequent burning, the grassland is more or less typical coastal prairie with mesquite dotted over it.

Chaparral Climax.—Chaparral differs essentially from the communities just considered in being truly intermediate between forest and grassland. It resembles them inasmuch as the majority of the dominants form root sprouts readily when cut or burned; as a rule they are browsed but little and none of them exhibit the ready migration of mesquite. As a climax, chaparral is at its optimum in California, where it is typically evergreen; toward the east it gradually loses this character, as well as much of its massiveness (48A).

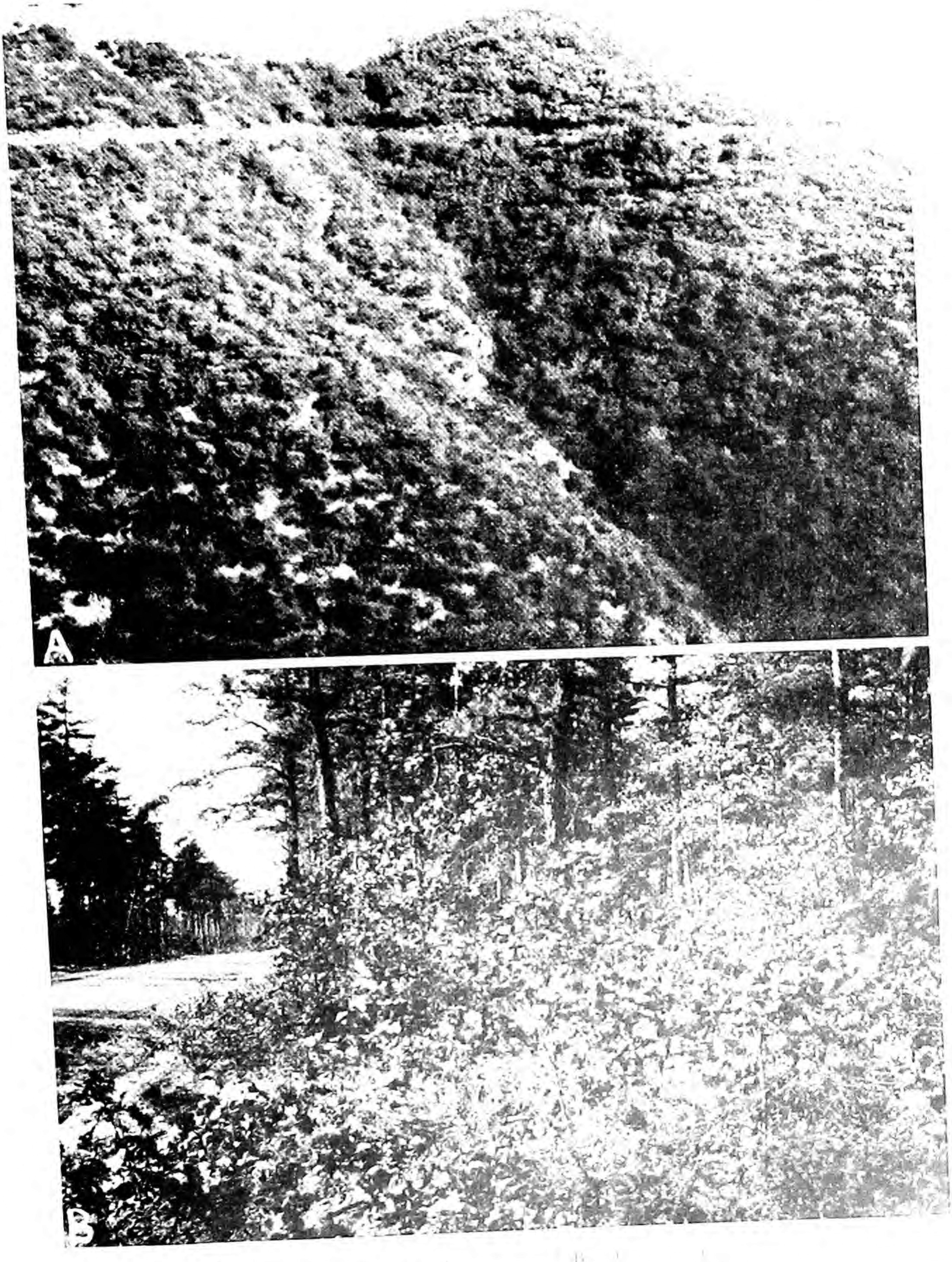
The interpretation of chaparral has been chiefly concerned with the question of its climax nature and its relation to grassland especially as to their relative extent in former times. The first could be solved only by an intimate analysis of the zone of scrub lying between the grassland and the montane forest. At the lower edge where it forms savanna with the bunch grass prairie, the dominants proved to be different as to genus and life form. It was soon realized that their affinities were with the sagebrush rather than chaparral and that they constituted a coastal association of the former, now chiefly represented by savanna. In the lower portion of the montane climax, the life form and genera were those of the chaparral proper, but the species were mostly different, constituting a fire subclimax destined to yield to coniferous forest. Between these two zones lies the mass of the climax chaparral, subject to recurring fires and regenerating rapidly and universally by means of root sprouts.

In the absence of the zone of coastal sagebrush, chaparral often lies in contact with bunch grass prairie and then forms a belt of savanna of varying width. This is chiefly true of its major dominant, *Adenostoma fasciculatum*, which is the most xeric constituent and hence occupies the lowermost position as a rule. Like most savanna shrubs, it maintains itself best in broken or rocky ground against the competition of grasses

and in such places forms small postclimax groups. During wet phases of major climatic cycles, *Adenostoma* and chaparral generally doubtless extended further down mountain-side and foothill, but the present relations have probably obtained since the last great pulsation of the Pleistocene.

The gradual encroachment of the grasses and a small amount of clearing have slightly diminished the area of chaparral during the historical period in California, but these processes have operated chiefly upon the coastal sagebrush. Fifteen years of field work has placed beyond question the conclusion that the spatial relations of grassland and chaparral have long been essentially what they are at present. The recording of many thousand grass relicts wherever the various types of protection exist renders it certain that the Sacramento and San Joaquin valleys, the many intermountain valleys, and the hills and lower ranges have belonged to the grassland climax for millennia past. This is supported by the universal absence of chaparral relicts in these regions and by historical records of the days of exploration, and finally confirmed by the course of competition between grass and scrub under protection.

Interpretation in Forest Climaxes.—The most important and fascinating questions in the interpretation of forest communities pertain to the nature and movement of climaxes. Because of the large number of forest climaxes and their location in regions of general or local glaciation, the problem is more complex than with either scrub or grassland, and it is further diversified by the long ecotones that these make with forest. Hence, it has been necessary to approach it from three different directions, namely: (1) reciprocal relicts within or between forest climaxes; (2) relicts in the ecotone between forest and grassland or scrub, and (3) those resulting from human coactions, chiefly fire or lumbering. However, in all of these the outcome follows the rule that life form and life history are the decisive features. Trees, like shrubs, are browsed, but this affects only the lower branches and has no significance except for seedlings or sprouts. Among trees themselves, the most striking difference is in response to fire, broad-leaved species as a rule sprouting readily, while this function is regularly absent in conifers, redwood being the most notable exception. Furthermore, some conifers are highly resistant to ordinary fires, as exemplified by *Pinus ponderosa* and *P. palustris* in particular. A few relicts are produced by fungus and insect coactions; the outstanding instance is that of *Castanea* and *Endothia*, the chestnut being


A
B

completely killed over wide areas or so badly damaged as to persist only in the form of root sprouts.

Deciduous Forest Climax.—Probably no other formation on the continent contains such a host of relicts in the form of preclimaxes and postclimaxes. This is due in part to the large number of dominants and the long ecotones between the three associations, arising from the fact that the maple-beech and chestnut-oak are enclosed on three sides by the oak-hickory community. More significant still is the marked dissection of the Appalachians and their flanking plateaus, such as the Cumberland and Allegheny, over which the various climaxes have moved in phalanx under the compulsion of glacial and interglacial climates. The mosaic of relicts has been further varied by the pathway afforded for the southward migration of the pine-hemlock and the spruce-balsam climaxes along the crest of the ranges.

As a consequence, the relatively xeric oak-hickory community appears as preclimaxes on xerocline slopes and ridges through much of the maple-beech and the chestnut-oak associations. Conversely, these more mesic communities constitute postclimaxes on mesoclines and in coves and valleys of the oak-hickory climax. Such intercalations or enclaves are especially numerous along the line of ecotones, but they frequently extend far into the mass of each association likewise, as exemplified by postclimax relicts of beech near the Gulf of Mexico. This wide distribution is probably to be explained by the greater compensatory effect of topography in the case of a climax flourishing within a rainfall of 40-60 in., by contrast with a range from 40-6 in. in the grassland climax.

The existence of relicts of white pine and hemlock in the maple-beech and chestnut-oak climaxes especially likewise reflects the compensating action of topography, though this includes temperature as well as water relations. Near their southern limit, postclimaxes of hemlock in particular require the protection afforded by both mesoclines and canyon-like valleys. Such relicts have usually been regarded as an intrinsic part of the surrounding deciduous climax, but this is a reflection of the static viewpoint. Not only is this view discounted by the life form, but it is also emphatically contradicted by the regular association of the hemlock and white pine in their climax region about the Great Lakes. This conclusion has been reinforced by the studies of hemlock relicts in Indiana by Friesner and Potzger (1932).

As the region of earliest and densest settlement by Europeans, the

deciduous forest has borne the brunt of human coactions in terms of fire, clearing and lumbering. These have wrought profound changes in the climaxes, often of such wide extent as to cause their reference to climatic or edaphic factors. The true explanation of the pine forests of the Southeast especially was first suggested by the detailed study of burn successions characterized by closed-cone pines in other parts of the country, notably *Pinus contorta* in Colorado and *P. divaricata* in Minnesota. Repeated reconnaissances through the coastal plain from New Jersey to Texas confirmed the similiarity of these subseres, and at the same time revealed the constant presence of relicts of the original climax of deciduous trees. In his studies of climax and sere in North Carolina, Wells had reached the same conclusion as to the climax, and this view was further supported by the work of Tharp in eastern Texas. In addition to oak-hickory relicts in all degrees of mixture with pines, there are frequent relicts of beech and other species postclimax to the oak-hickory in this region.

A recent analysis of the several burn consocies from New Jersey to southern Florida and west to Texas has left no doubt that this region belongs to the oak-hickory climax and that the abundant hardwood relicts would again take possession under proper protection, especially from fire (1932). This journey was made during a drouth period in which fire was almost universal, and the paramount significance of this process was much more convincing than it could have been at any other time. Explicit testimony to the paramount role of fire was also discovered in the so-called "plains" of New Jersey, which are barrens clothed with a dwarfed spreading life form a few feet tall. To the student of succession, this was obviously an effect of fire, a conclusion confirmed by finding the same adaptation in a recent burn surrounded by tall pines and relict oaks (Plate 48B). The universal role of fire in the Southeast was further attested by the grass and heath balds of the Great Smoky Mountains. Various causes have been advanced in explanation of these, but the constant and especially the recent evidences of fire place beyond question the fact that they represent subclimaxes in the burn subsere.

Frequent reference has been made to the relicts of the oak-hickory climax that front the prairie or still linger in it. These are the most conspicuous and in some respects the most eloquent of relict communities, chiefly because of the differences in the life forms and climatic relations of the respective dominants. In the widespread shrinkage of the decidu-

ous forest before advancing desiccation, advantage was taken of every compensating feature, and this serves to explain the numerous fringing forests of streams from Saskatchewan to Texas, the unique relicts in deep cool canyons, and the climax-like savannas of mountain outliers and sandy plains in Oklahoma and Texas.

The most dramatic event of the period of desiccation was the falling back of the forest along the line of the isohyet of 40 in., running from central Missouri through southern Illinois and into Indiana. The spearhead of the prairie advance reached Ohio and southern Michigan, where a few relict areas still persist. From here westward to the Mississippi the hold exerted by the grasses through competition has delayed the return of forest, and through the period of settlement, fire and clearing have co-operated to make this slower and in many places impossible. In consequence, this great wedge of subclimax prairie will long be represented by relict areas within the climate of forest—perhaps indeed until both forest and prairie have practically vanished before cultivation.

Coniferous Climaxes.—On the west, the contact between prairie and forest is regularly constituted by conifers. The most extensive ecotone is that between mixed prairie and woodland consisting of juniper and pinyon (*Pinus edulis*). Like the oak-hickory forest, this has undergone extensive shrinkage as a result of desiccation, and over three-fourths of its area exists only in the form of savanna in a grassland climate. Relicts of the actual climax still persist at higher elevations in sufficient number and mass to serve as a basis for tracing the process of shrinkage and the concomitant invasion by the grassland. In the task of interpretation, however, it has been necessary to reckon with two facts of importance. The one is the ability of the woodland dominants to invade talus slopes earlier than the grasses, only to be replaced by the latter, and the other the facility with which juniper increases in density and extent as a consequence of dissemination by birds, sheep, and goats into areas where the occupation of grasses is much weakened by overgrazing. In California, the annual dry season has emphasized the effects of desiccation, and the woodland exists today only in savanna form or isolated fragments, in which the Joshua tree (*Yucca brevifolia*) is sometimes a unique dominant.

Along the central mountain ranges, the woodland is absent and the advancing grassland has taken the places left by the vanishing pines (*Pinus ponderosa* and its varieties). The process of shrinkage is similar

in all essentials to that for woodland, and the outcome is likewise the production of a broad belt of savanna. On the east, three great relicts still persist, two of them in the form of plateau savanna on Cheyenne Ridge and Pine Ridge in western Nebraska. The other occurs as pine climax in the Black Hills of South Dakota, where it is associated with relicts from the boreal climax, namely, *Picea canadensis, Betula alba papyrifera* and *Populus tremuloides.* In California, the withdrawal of the yellow pine has apparently led to the evolution from it of a relict species (*Pinus torreyana*), now surviving only around the Soledad Estuary at La Jolla and on Santa Rosa Island near Santa Barbara.

A similar evolution of new species from the dominants of shrinking climaxes has been a remarkable feature of climatic changes in California. Apart from the universally known *Sequoia gigantea* and *sempervirens,* these comprise five pines, viz. *Pinus radiata* and its variety *binata, muricata, attenuata, sabiniana* and *coulteri,* five cypresses, *Cupressus macrocarpa, goveniana, guadalupensis, macnabiana* and *sargenti, Pseudotsuga macrocarpa* and *Abies venusta.* The position of all of these in terms of latitude and altitude would indicate that they have developed under more xeric conditions than those in which their probable ancestors dwelt and that a continued shift toward desiccation has resulted in isolation and shrinkage, which have nearly led to extinction in the case of *Pinus torreyana, P. radiata* and the species of *Cupressus.* It is not improbable that several other species of restricted area on the Pacific Coast have passed through a similar history, for example, *Pinus lambertiana, P. jeffreyi, Picea breweriana, Abies magnifica* and *Chamaecyparis lawsoniana.* In this connection, it is interesting and possibly significant that the southeastern United States exhibits a group of several endemic species of pine, and the southern Appalachians the apparently relict *Tsuga caroliniana* and *Abies fraseri.* In all of the species mentioned, evolution and restriction are most plausibly related to the southward migration of the ancestral stock or to later shrinkage under a warmer or drier phase of a major cycle.

Natural Areas and Research Reserves

While national forests and grazing reserves have afforded opportunity for much ecological investigation, this has necessarily been focused in large degree upon regulated utilization. With the rapid accession of

interest in natural and wilderness areas and in research reserves, a new vista is opened to scientific research in national and state parks, national forests and similar preserves. To realize this adequately, the methods of dynamic quantitative ecology are indispensable, and a comprehensive system has been developed for this purpose. This rests upon the biome as the basic unit and upon climax and succession as the two paramount objectives. It employs the relict method as the key to both the past and the future, and places proper emphasis upon the measurement and record of community functions and changes by means of quadrats and exclosures.

The essential features of such an ecological system are: (1) reconnaissance of the area, (2) selection of particular communities or portions, (3) detailed survey, (4) installations for exclosure and experiment, (5) records in the form of maps, notes, charts and photographs to serve as standards, for (6) valuation study and resurvey at intervals of five to ten years. Perhaps the greatest lack of dynamic ecology has been the continuous tracing of succession and other changes, because of the length of time involved, the absence of control over desirable communities, and the difficulty of securing long-term co-operation. With the establishment of research reserves of various types, the first two handicaps disappear and the solution of the third becomes the sole problem, which demands immediate attention. This is now being given in America and it is noteworthy that a beginning in this respect has been made in the Antipodes at Arthur's Pass, a national forest of New Zealand.

Chapter VI

CLIMAXES, SUCCESSION AND CONSERVATION

Importance and Methods of Study.—New and cogent reasons for the detailed study of climaxes and succession are to be found in the significance of these for great public projects, especially in connection with erosion and flood control, and the reconversion of so-called marginal lands to range and forest. As the product and indicator of its climate, each climax provides an index to the proper utilization of the land and hence points the way to the rehabilitation of cut-overs, dry-land farms, "blow"-areas and overgrazed ranges. All of these are likewise marked by successions due to disturbance, which serve as trustworthy guides to the details of restorative processes.

For these reasons, field reconnaissance has been focused chiefly upon those regions in which public projects are under way, particularly those concerned with erosion and floods. In this connection the climatic communities of the first importance are the grasslands of the West and the deciduous forests of the East, together with the pinelands of the South. All of these have been cleared or broken in large measure or much modified by various types of disturbance, with the consequence that the method of relicts must be constantly called into requisition for the reconstruction of the climax. Applied to the true prairie of the Middle West, this has shown that the tall *Andropogons* are really invaders from the postclimax meadows, and a further survey on this basis indicates that practically all of Iowa, southernmost Wisconsin and northwestern and central Illinois are to be assigned to the true prairie, a conclusion in closer accord with the rainfall-evaporation values. As a consequence, the subclimax, or better, postclimax tall grass prairie proper is restricted to the general vicinity of the margin of the deciduous forest, occurring likewise in extensive "openings" well to the eastward.

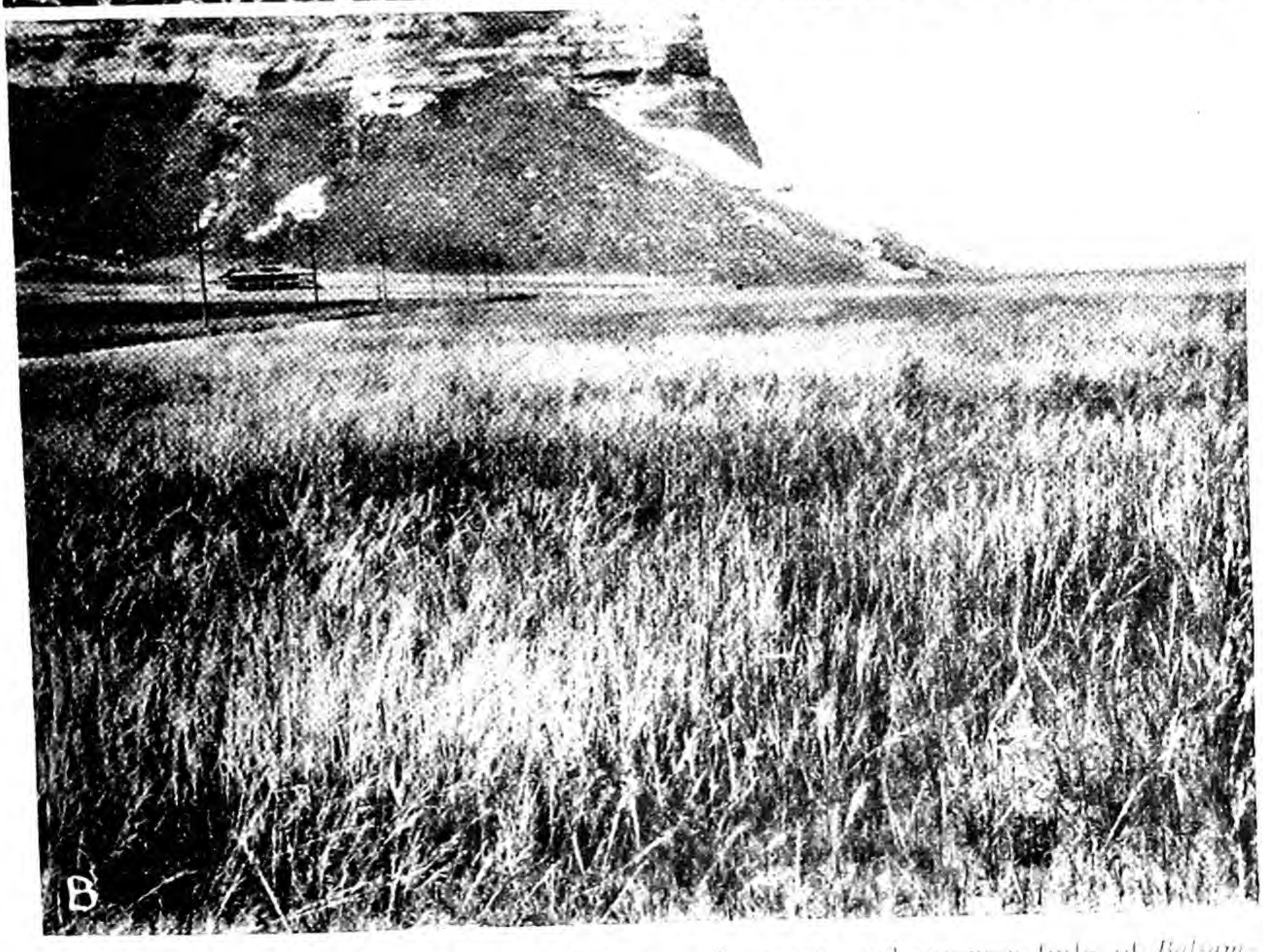
The contrast between agricultural practice and erosion processes in California and the Palouse region of Washington arises from the type of precipitation, which is reflected in two different associations of bunch grass prairie. A re-survey of these from southern California to central Washington and eastward into the mixed prairie of Montana, Wyoming

and Colorado has served to bring out more clearly the climatic and edaphic relations of the dominants and to furnish an adequate basis for the control of water erosion and flooding in California, and of wind erosion in the Palouse.

Relationship of Palouse and Mixed Prairie.—While the term Palouse refers to a particular region of the Northwest, its use is justified for the more extensive climax association, in which the striking bunch grasses, *Agropyrum spicatum* and its variety *inerme*, are the characteristic dominants. It seems probable that the derivation of these from the widespread *A. smithi* was caused by a shift toward winter precipitation, which set apart the climate and climax of the Palouse region. This appears to have been a relatively recent event, since practically all the other dominants are those of the mixed prairie and the transition between the two is unusually broad. This is due in large measure to the basin-and-range topography, in which dovetailing on the two levels is a typical phenomenon. In consequence, it becomes necessary to recognize two divisions or faciations, namely, the Palouse prairie proper of southeastern Washington and adjacent Idaho and Oregon, and the outlying transition, in which the dominants of the mixed prairie assume a rank equal to that of *Agropyrum spicatum*. This extends from northern California and Nevada through all of nonforested Idaho and for some distance into Montana and Utah. A similar shift occurs along the southern boundary of British Columbia, but the details of this are still to be worked out (Plate 49A).

In general, the divisions or associations of the grassland climax correspond to rainfall differences, while the subdivisions or faciations are chiefly the outcome of temperature contrasts. As a result, faciations may assume both an altitudinal and latitudinal expression; for example the submontane type of mixed prairie in the central Great Plains has its counterpart at moderate levels in central Alberta and Saskatchewan. It is significant that the dominant grasses which mark this cooler faciation should all be of the circumpolar type, namely, *Agropyrum pauciflorum*, *Koeleria cristata*, *Festuca ovina*, and *F. scabrella*. Meanwhile, such typical southern species as *Bouteloua gracilis* and *Buchloe dactyloides* have disappeared, the latter below the international boundary, while blue grama may survive as a relict much farther north (Plate 49B).

Types and Roles of Short Grasses.—In the further analysis of life forms as indicators of factors and processes, it has become clear that the

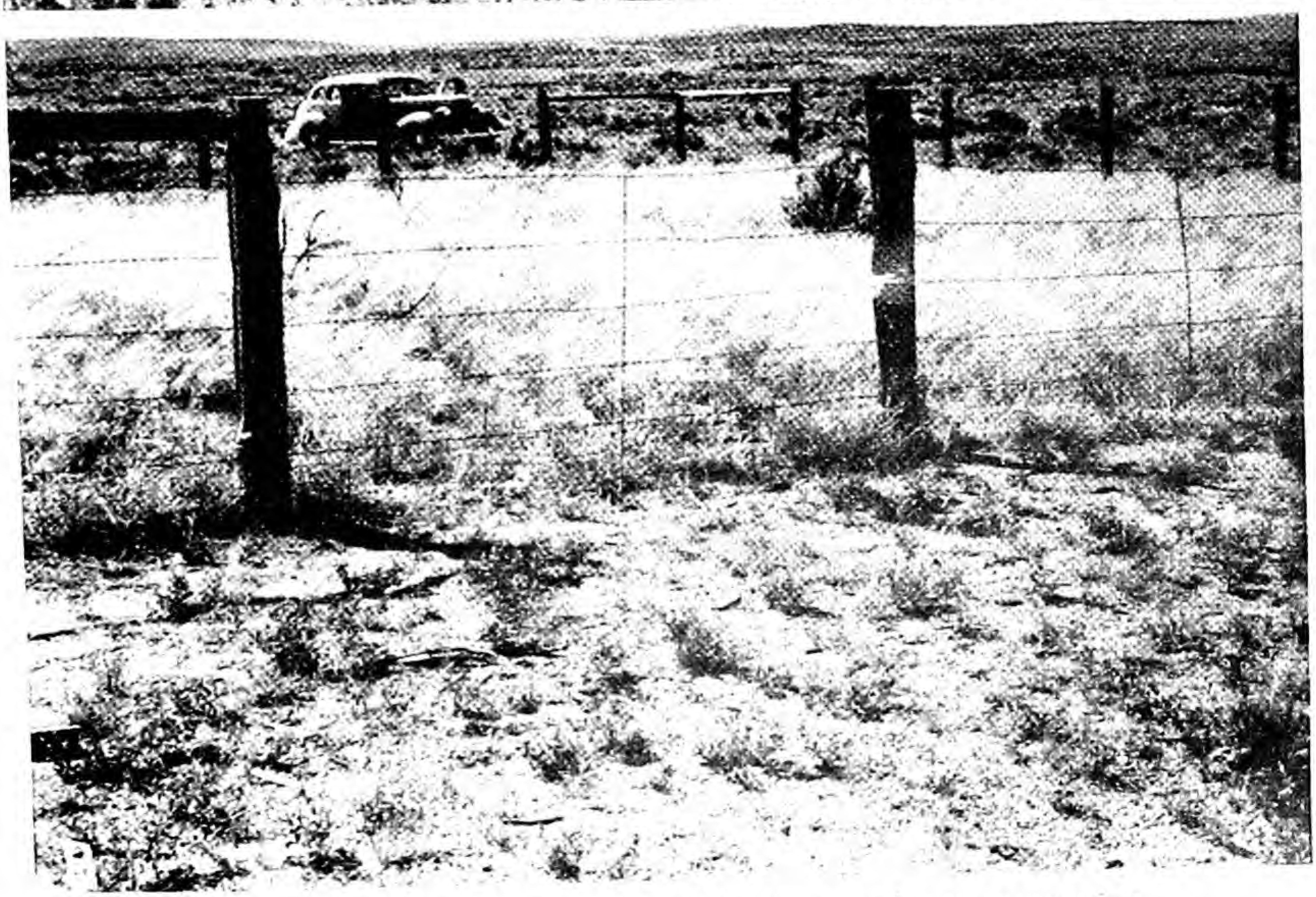


A. Palouse prairie with *Agropyrum* and *Festuca* dominant, and common forbs of *Balsamorrhiza, Achillea,* etc., Moscow, Idaho. (Photograph by J. E. Weaver.)
B. Mixed prairie of *Stipa, Bouteloua, Agropyrum,* etc., Scott's Bluff, Nebraska.

term short grass covers a number of subforms, quite apart from the well-known sod and bunch types. The best known and most typical are species of *Bouteloua* and *Aristida*, together with *Buchloe* and *Hilaria cenchroides*. These are southwestern in origin and their low stature denotes the impress of a subtropical climate. They have moved northward into the mixed prairie during dry phases that simulate their original climate and have persisted as an open under-story to produce the well-known short grass plains during the grazing period. A second type, the short sedges, have accompanied the boreal grasses in their migration from circumpolar regions. The two more important are *Carex filifolia* and *stenophylla*, found in the Palouse as well as the mixed prairie, where their ranges overlap those of the gramas. In spite of their northern origin, they are more xeric than grama and buffalo grass, and they persist westward to characterize the driest faciation of the mixed prairie. When the associated mid grasses are grazed off, these sedges form a short grass disclimax, similar to that of the Great Plains, in which they may also occur.

Much as *Carex* replaces *Bouteloua* in the drier districts, so the small forms of the boreal *Poa*, such as *scabrella*, *secunda*, and *arida*, play a similar role in the cooler North, where grama is less abundant or absent. However, these are more delicate plants with poorer root-systems, after the fashion of annuals, and are more easily replaced by the mid grasses when these are released from heavy grazing pressure. The fourth type comprises true annuals, of which *Bromus tectorum* is the best example. Under severe grazing, its reduced stature, high seed production, and early development make it the ultimate winner wherever it obtains a foothold. In the past quarter century it has swept across the Palouse into the Great Plains, where it can only be checked by fostering and replacing the native perennials (Plate 36A).

The Sagebrush Disclimax.—As disturbance communities produced by man, the various disclimaxes indicate not only the course of deterioration, but also the processes necessary to rehabilitation. This is perhaps best exemplified by sagebrush, the vast extent of which lends color to the plausible assumption that it forms a climax. The several types of evidence were invoked two decades ago to confirm the hypothesis that *Artemisia tridentata* had advanced from the Southwest in a dry phase and retreated during a moist one, to leave an open savanna over the major portion of the Great Basin. This view was supported by relict



A. Sagebrush disclimax near Colorado Springs, due to overgrazing
B. *Stipa comata* in a 6-year exclosure in burned sagebrush, Idaho

patches of Palouse or mixed prairie wherever protection against grazing occurred, by numerous observations through the climatic cycle of the effects of grazing and of fire, and by the testimony of early explorers and ranchers. These were supplemented by preliminary experiments, which demonstrated that overgrazing depleted the grass and increased the sagebrush, while protection or removal by fire, grubbing or dragging again gave the grasses the upper hand in the competition (Plate 50A).

This testimony has been greatly reinforced by demonstrations carried on by the Forest Service and the Soil Conservation Service, as well as through increased burning by the stockmen themselves. Such results are now so numerous and extensive as to leave no doubt that over most of its area sagebrush is not a climax at all, but a consequence of disturbance. Since it rarely forms root-sprouts, sagebrush may be almost completely eliminated by fire, the climax grasses reappearing in normal condition after two or three years and persisting as long as grazing is regulated. Some seeds survive all but the severest fires and thus serve to maintain an open savanna such as existed before the grazing period (Plate 50B).

The reduction of the grass and the development of a sagebrush disclimax does not make the range entirely valueless for grazing. Sagebrush furnishes considerable winter browse, provides insurance against drouth and holds drifting snow. Hence the tests by means of experimental grids are based upon the desirability of leaving unburned strips to secure these values. Since sagebrush has but moderate usefulness for erosion control, grids are also designed to determine the need of reinforcing it with contour trenches. The question of the proper balance between climax and disclimax species constitutes one of the most important problems in conservation and must be taken into account in all field demonstrations and experiments. Theoretically, when it is a choice between climax and disclimax, the former will regularly give the highest sum of values, but as just suggested, some combination of the two may yield a wider range of values, as well as require less effort for its maintenance.

Nature and Origin of Aspen Parkland.—The broad ecotone from the prairie to the boreal forest of Canada is marked by groves of aspen that increase in size and extent to the north, where they merge with the spruces. In view of the effect of fire upon forest, it has been a natural assumption that parkland is the rear guard of a retreating climax. This

is not only contrary to the opinion of settlers, who believe the aspens to be advancing, but is likewise refuted by the general behavior of deciduous woodland when burned in contact with grasses. Since the great majority of hardwoods are able to form root-sprouts after fire or cutting, such stands may be reduced to scrub, but are rarely if ever eliminated, even by annual burning. In fact, the regular effect of fire is to favor shrubs and trees at the expense of grass, with the consequence that not only do the aspen groves increase in size, but new ones also develop along the border. Extension is also brought about by grazing and to some degree by cultivation, which tends to restrict itself to the prairie.

The term parkland has the advantage of being indigenous, but is not strictly accurate ecologically, since the aspens form dense copses or motts, instead of being scattered in true parks or savanna. It is probable that two processes contributed to the original formation of parkland, which is postclimax to the prairie. The first was the lagging of the aspens as the boreal forest straggled northward after a climatic shift to the warm-dry phase, and the second the effect of grass fires along the front, which took a heavy toll of the conifers. Today the groves comprise a tall central mass encircled by two or three zones of fire saplings, while fire scars are frequent on the trees. Rodents have been supposed to play a part in the spread of seedlings from the parent groves, but their contribution is quite insignificant (Plate 51A).

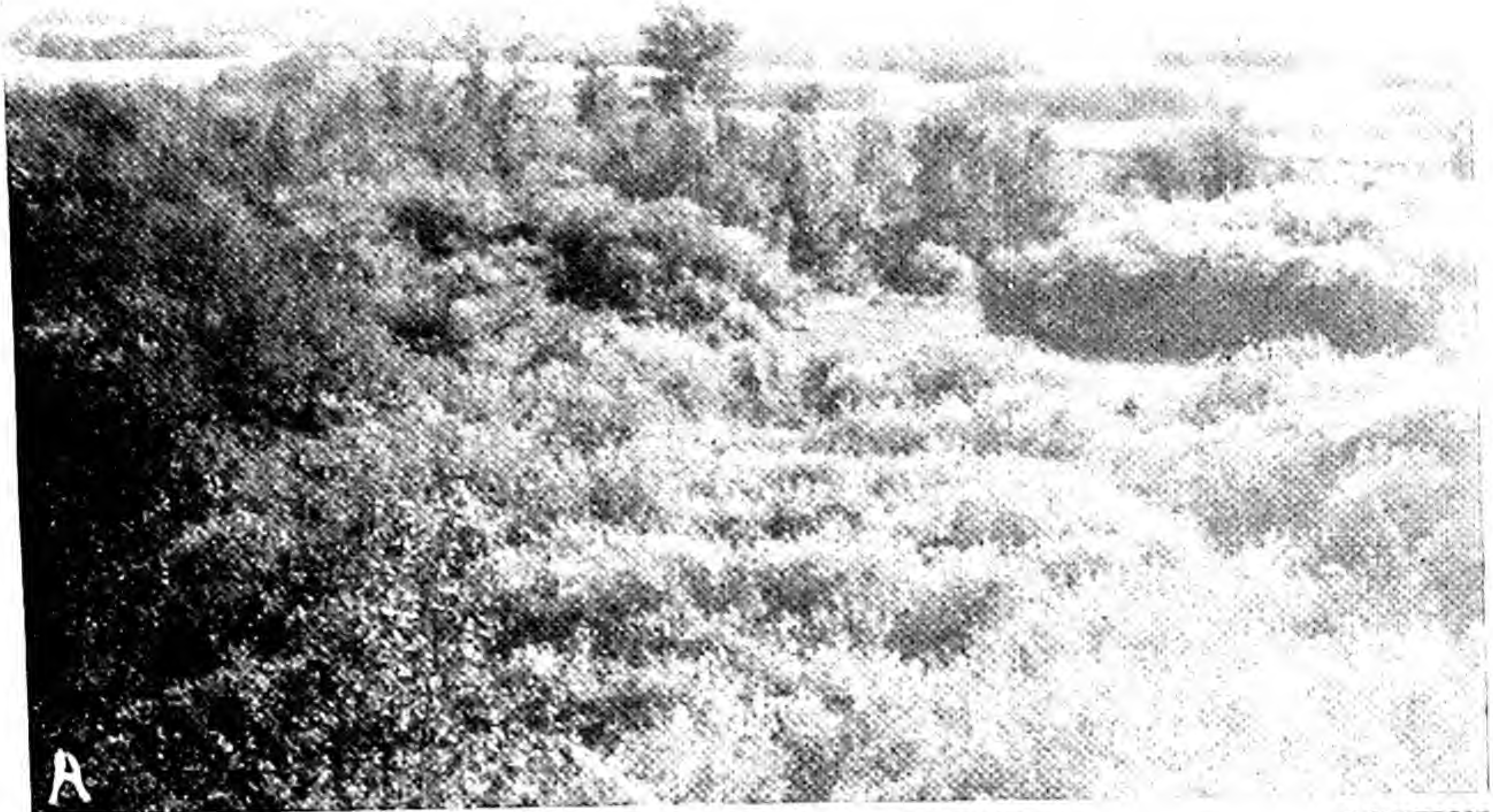
Such an analysis of aspen parkland brings this disclimax into harmony with all the others that have encroached upon the prairies. These are oak-hickory woodland in the East, mesquite and desert scrub in the Southwest, chaparral along the mountain fronts, and sagebrush in the Great Basin. Migration by climatic compulsion has carried trees and shrubs into the grassland, and the laggards at the next turn of the cycle have supplied the relicts upon which man has operated through fire, grazing and cultivation.

The Origin and Nature of Oak Barrens and Openings.—From time to time these peculiar communities of the oak-hickory association of the deciduous climax have been studied in the course of field trips through the East, and an opportunity was found to compare them more in detail in the autumn of 1939. The floristics of the oak openings in Ohio have been extensively treated by Moseley, and the Kentucky barrens have been comprehensively discussed by Dicken. In spite of the difference in

name and the marked divergence of the soils, these are much alike in origin, in climatic and seral relations, in composition and in problems of utilization. In essence, they are inclusions of the tall grass postclimax swept into the deciduous forest from the Southwest during the major warm-dry phase of the post-Pleistocene. With the return of the cool-moist forest climate, the grasses found refuge in the shallow limestone soils of the barrens or the sands of the openings, where conditions favored them in competition with trees (Plates 38A and 48B). How narrow this advantage is, may be readily seen from the invasion of small trees and shrubs in both communities, and there must always have been a successional trend toward the climax, fluctuating with the climatic cycle and often upset or much modified by man. A similar phenomenon is to be observed in the Indiana dunes about Lake Michigan today, but the succession is still active and hence the stages are much more distinct. The same general relation of forest to prairie now prevails throughout the ecotone between them. What seems to be the same but is actually a reversed relation characterizes the Cross Timbers of Texas and the similar woodlands of Oklahoma, in which sand has provided trees with the needed compensation against a prairie climax (Plate 51B).

The origin of the prairie was a topic much debated before the rise of dynamic ecology, and various explanations continue to be offered by those little or not at all versed in vegetation. The evidence from paleo-ecology, however, permits no doubt that the prairie, like other great climaxes, is a product of climate and as such has been in existence some millions of years. Throughout this time, it has been subject to climatic shifts and has moved forward or backward under the compulsion of warm-dry or cool-moist phases of major climatic cycles. Chief among these have been glacial-interglacial cycles, and the present distribution of the prairie bears the impress of the latest of these. As a consequence, prairie inclusions are still to be found far beyond their proper climate and have been a perennial puzzle to those unfamiliar with the history of vegetation.

As such a great relict area, the barrens of Kentucky and neighboring states have been the object of all possible interpretations, among which fire has easily ranked first. Fire, however, could not have originated the grassy tracts, nor could it have extended them, since years of annual fires can do no more than reduce hardwoods to the condition of scrub. Clearing could have had only a secondary minor effect, and the herds



A. Overlook of aspen parkland to spruce climax near Edmonton, Canada.
B. Cross timbers of Postoak and Blackjack, with little and big bluestem, Indian grass, etc., on sandy soil, Decatur, Texas. Soil Conservation Service.

of buffalo practically none at all. By far the most probable course of events was a climatic change toward dryness, marked by the forward movement of prairie, followed by a return of the moist forest climate (a rainfall of 45 to 50 inches), the persistence of grassland areas on shallow limestone soil, readily dried by widespread underdrainage, the formation of swamps, especially canebrakes, followed by succession to savanna, and finally a wide range of disturbance effects, of which cultivation and fire were the chief.

A Method of Compensation for Drouth.—Though drouth periods are now known to be recurrent and inevitable, it is not yet realized that the methods of compensation and conservation available are adequate to eliminate their major effects. The various processes concerned have been developed independently, and the present need is to organize them into a complete system for minimizing drouth. The first task is to bring about their proper coordination, and this can be done only by practical tests, such as have been proposed.

An adequate system of compensation must take into consideration the advance made in long-range forecasting since 1930. In this period the predictions of monsoon rains in India have achieved a rating of 82 percent, and this record has been approached by several investigators in the United States. The present need is to test the various indices in a much larger number of areas and regions and to determine their value for anticipating seasonal distribution as well as the annual departure. In addition to rainfall, it is possible to forecast temperatures and consequent evaporation, both of which are concerned in the fate of the water that enters the soil. The amount of moisture in the soil at any time is easily determined and, with the record of its changes from time to time, affords an invaluable prediction of probable crop yields. The most striking application of this method has been to fields of winter wheat with summer fallow, where it all but insures the equivalent of an average annual crop, but it can be applied with similar success to other cultivated and native crops.

In dry years or arid regions, only about a third of the rain that falls becomes available to plant roots. The major portion is lost through interception, runoff and evaporation from the soil surface. Loss by interception is governed by the type of rain and the kind of cover, and is practically unavoidable. On the other hand, runoff may be reduced to the vanishing point, and evaporation may be cut down to a fourth or

less of the normal. Such savings constitute the direct compensation for drouth and aridity; appropriate measures have been extensively developed and only await decisive test through incorporation in the compensating system. The problem of filtering water into the soil, with corresponding control of runoff, erosion and flooding, has been largely solved and the process only requires certain refinements. At present these involve chiefly the interaction of cover and intimate structures, such as small furrows or trenches, though ultimately the major reliance will be placed upon plant life. In the steps to be taken for reducing evaporation losses from the soil, stubble, straw, hay and dry weeds constitute the outstanding materials. Dead rooted cover surpasses all other types of mulch in total effectiveness when penetration, control of wind and water, evaporation and transpiration losses are taken into account.

In the study of succession in abandoned fields, recovery was found to be far more rapid after the sketchy tillage of the "suitcase farmer" than elsewhere. Shallow ploughing at the outset and the practice of drilling seed for the next wheat crop into the headed stubble without further cultivation explained the good tilth and the persistence of grass crowns and rhizomes. What was generally regarded as a shiftless practice was actually a new way of securing the values just mentioned, and in addition a fair control of weeds with their high transpiration waste (Plate 59B). It was further assumed that this control could be rendered nearly as complete as that with bare summer fallow by using a subtiller blade to sever the roots and at the same time loosen the soil without turning it up. An additional advantage is that of maintaining the soil profile in its optimum nutrient relations, a factor too often overlooked in the traditional "good" tillage. For this purpose several implements are now available, but the most satisfactory are those that leave the headed stubble upright. With sufficient draft, it will become feasible to carry out harvesting and subtilling in one operation.

Two other features of critical import are, first, a prompt and accurate soil and land-use survey, by which crop lands may be set aside from range or fields to be regrassed; second, crop adjustment to the soil-water capital and the probable rainfall, together with crop specialization, which is already well advanced through the efforts of the various experiment stations. Finally, application of the principles and methods of bio-ecology is essential to the treatment of each farm as an organized unit, and has definite though indirect effect in minimizing the impact

of drouth, both economically and socially. Control of rodents and predators of all kinds, game management for waterfowl, quail, grouse, and pheasants, ponds for fish, muskrats and beaver, and proper stocking of the various domestic animals will afford full scope for establishing a working balance between plants and animals on the farmstead.

The Biotic Significance of Disturbance.—Field observations to the effect that rodents in general prefer disturbed areas in grassland have been confirmed by the results from rodent-proof exclosures, in northern Arizona especially. These regularly contain a larger percentage of forbs than does the range outside or the cattle-proof unit which is open to rodents. After the forbs had disappeared from the latter, a small plot was fenced with hardware cloth, and the forbs reappeared in a few years, only to vanish again when the fence was removed. The preferences of prairie dogs have also been determined by noting the various species utilized for food. In one large town in the mixed prairie, 15 species had been eaten to some degreee, whereas none of the grasses had so far been touched. This by no means signifies that rodents do not consume grass, but the latter seem to be a second choice, except when forbs are few or hard, or a protected range adjoins a depleted area. A novel instance of this fact has occurred in recent years of drouth, during which pocket gophers have moved out of pastures and meadows in large numbers, to occupy the better-watered, greener shoulders and shallow ditches of roadsides. In some cases the mounds are almost continuous, with a high density for a score or more of miles, constituting an infestation such as has never been observed in natural cover (Plate 52A).

The initial disturbance that leads to the invasion or increase of rodents usually results in renewed disturbance on a larger scale, which brings about a disclimax more or less typical of the species concerned. Though the change in composition may be pronounced, such areas are relatively insignificant and temporary, and commonly return to the climax condition within a few years after abandonment. No matter how great the control may seem at the maximum, all the grazing animals, from prairie dog and jackrabbit to antelope and bison, wild horses and cattle, exert only a transient effect upon the climax. Their major influence is due to coaction and hence they are known as influents, in contrast with the plant dominants, which owe their mastery of the climax to reaction upon the habitat (Plate 52B).

The Ecological Basis for Regrassing. Throughout the grassland

A. Pocket-gopher mounds along roadside; near Bridgeport, Oklahoma
B. *Dalea spinosa* dying as a result of the work of kangaroo-rats; Glamis, California

climate and climax, the grass cover will be restored by the natural process of succession when the disturbance ceases wholly or in large part. The rate at which this restoration takes place depends primarily upon the supply of seeds or other parts; it is rapid wherever rootstocks have persisted in the soil, and exceedingly slow when seeds must come in from neighboring pastures and roadsides, as is the usual case. The rigor of conditions as to germination and seedling establishment often plays a decisive part likewise, notably in the hot, dry desert plains of the Southwest. On the lower levels of this association, the grass relicts are so small and few, the soil is so depleted by erosion, and temperature and evaporation are so excessive that succession is all but impossible, and the disclimax desert scrub will remain in possession for a long time to come. In consequence, natural succession can be depended upon for recovery only under exceptional circumstances, and for rapid restoration must be supplanted by artificial methods that speed it up greatly.

However, the requirements for success with artificial succession are essentially identical with those for the natural process. The ruling disturbance must be stopped, as well as such accessory ones as grazing and rodent action; seed must be supplied in large amount and properly planted, infiltration increased, erosion and evaporation diminished, and competition reduced to a minimum. The probability of securing an adequate stand will be enhanced if seeding is done in the light of the record of soil moisture and with some consideration of the rainfall cycle in general and the special pattern of the region concerned. The ecological rule is to reproduce the natural process in essentials but to telescope the stages into two or three at the most by controlling conditions and greatly increasing the seed supply. In the case of such vigorous colonizers as sand-dropseed or crested wheatgrass, a dense, pure stand may be obtained the first year in the proper climate for each, but this will probably not be the final stage.

A significant corollary to the principle of adaptation is to the effect that native species, particularly climax grasses, are better suited to their particular subclimate than are alien ones. This not only is logical from the theoretical standpoint, but also derives strong support from the results of a quarter-century in transplant gardens. It is also confirmed by the behavior of grass populations of one species drawn from different portions of its range. Thus, seeds of blue grama from the northern Great Plains have been found to germinate and to bloom and set seed

A. Crested wheatgrass drilled in; near Madras, Oregon
B. *Elymus* broadcast in field near Colorado Springs

earlier than those from the southern, and the plants are but a third or a fourth the size. Plants from intermediate stations only a few hundred miles apart form distinct intergrades in all these respects. These constitute characteristics of less fixity within the more permanent climatic pattern fixed much earlier in terms of boreal or northern ("winter") grasses and subtropical or southern ("summer") ones. The extent to which climatic and edaphic strains can be modified by different environments is now being investigated on a much larger scale by means of regional grids.

A different type of restoration, but one equally entitled to the term regrassing, has been well justified by the initial experiments and is now on the eve of being widely extended by means of the grid method. This is the re-establishment of climax grassland by burning off the sagebrush, which today forms the characteristic disclimax of the Great Basin and extends well beyond its borders. No other method can compare with this in the quickness and cheapness with which a vast acreage can be returned to productive grassland. This is said with full realization that fire is a dangerous tool and should never be employed except under competent and experienced direction. Regions differ much, however, in physical conditions, in the age and stand of sagebrush, in the quantity and species of the grass relicts, and in the grazing system. Most critical of all perhaps is the time of burning, with respect to the rate at which the fire runs and the risk of injury to the grass. The immediate task is to perfect the method of burning for each distinct area by means of adequate grid installations and then to proceed with the practical program as rapidly as grazing demands warrant. (Plate 50B).

The Role of Cover in Conservation.—The climatic cycle of the decade between 1930 and 1940 has recapitulated in miniature the much larger cycles of postglacial times and the more remote geological past. This is particularly true of the protracted drouth phase with its marked effect upon vegetation and soil, and the human responses that depend upon them. The period has not been sufficiently long for vegetation to exhibit migration on the same large scale as in the past, but local migration, destruction of species populations, changes of composition, and modification of form have all occurred in prairie and plains since the advent of dry years. These have furnished support in dynamic terms to the basic ecological thesis that the major communities of the globe and their constituent species are responses to the great climates and that

they migrate and evolve as the climates shift during long periods. In other words, each climax, as well as its more recent subdivisions, springs from an earlier vegetation through the further evolution of its dominant species under climatic stress.

To understand the role of cover both as an object of conservation and as the chief method in it, it has been necessary to turn to the life form and life history of the major species, as well as to the dynamic processes concerned in succession. For example, in the mixed prairie of the Great Plains, each important species or dominant possesses its own habit of growth and growth form, exerts its particular reaction upon the soil and upon water, and manifests its own type of competition and co-operation with the associated dominants. They form an organic whole, in which no one part can be changed or removed without affecting all the others, a principle that has served to explain some unexpected results in attempting to modify or restore cover in conservation projects. Succession, both climatic and edaphic, is a universal and inescapable process, and its detailed course must be understood to permit its control or guidance. The general significance of all these features to the restoring of overgrazed pastures and to recovery in abandoned fields has already been pointed out. Much attention has also been given to methods of supplementing the natural processes by means of furrows and trenches, which promise to shorten greatly the length of time necessary for succession.

The installation of the pasture furrow by the Soil Conservation Service has been carried out on such a vast scale, amounting to many thousands of miles, that it has been possible to study its performance in practically all the grassland communities. The results have confirmed the assumptions drawn from the ecological investigation of dynamic processes in each type. In a complete grass cover, the stems and leaves intercept some part of the rain and together with the litter retard movement so that nearly all the water is led into the soil by means of the roots. Under such conditions, the silt and fine organic matter are held in position to maintain the normal soil structure. Cover exerts a similar control of the surface soil by reducing or eliminating the force of wind. These desirable effects are diminished as the cover is impaired by grazing, fire, or drouth, and it becomes essential to reinforce the grasses by means of mechanical aids.

The primary question thus becomes one of the size and spacing of the

Disadvantages of large furrows:
A. Large amount of soil taken out of production.
B. Invasion of furrow by weeds.

furrow to be employed. Sheet erosion, gullying, and flooding must be prevented, water and nutrients retained and absorbed into the soil, favorable conditions provided for the germination of seed, and the soil disturbed as little as possible, in order to prevent a succession of weeds. Large contour furrows meet these requirements more or less imperfectly, since their chief value lies in holding back heavy rains to prevent accumulation into flood proportions. With spacings of 30 to 100 feet, too much water drains into the ditch and away from the slope where is it needed, carrying with it silt and organic matter. The ditch first becomes a pond, then a mass of colloidal material, and finally a miniature desert with an almost impervious soil, in which seedlings soon perish. The ridge or berm washes into the furrow on one side and over the grass on the other, and this bare area becomes the site of a weedy growth, of little or no value as forage or protection and barring out grasses for a number of years to come. When western wheatgrass or buffalo grass is present, a thin band of regeneration may appear at the edges of the ditch and the base of the berm, but this is of little importance by comparison with the width of the drained interval. Furthermore the amount of surface taken out of production by furrow and ridge may exceed 20 per cent when the interval is 20-30 feet, thus rendering the furrow still less adequate to the needs (Plate 54).

In the task of remedying the defects of large furrows, the experimental plots have been based upon the assumption that the best device will hold practically all the rain where it falls, at the same time preventing washing of the fine surface material. Other desirable effects are to spread the soil so that it serves as fertilizer instead of burying a wide band of cover, to leave roots exposed in the trench to act as channels of absorption, and to prune the roots and thus stimulate their growth. Finally, the shallow trenches catch seeds and litter and form excellent seed beds. In the initial tests, the intervals were set at 6, 3, and 1.5 feet, and the trenches were respectively 6x4, 4x3 and 3x2 inches wide and deep. The outcome indicates that the closest spacing produces the best results in accordance with the expectation, and that the larger dimensions are best for the trench, depending in some degree upon soil and condition of cover. It has also been found that much the most rapid recovery occurs when sod grasses are present, and this suggests the desirability of transplanting wheatgrass or buffalo grass to treated areas where they are absent. In terms of time, labor, and equipment, trenches or "corruga-

A. Dunes formed by soil blown from abandoned fields during drouth of 1934-35. Dalhart, Texas.—Soil Conservation Service.

B. Soil of the same area stabilized by vegetation planted after the dunes had been leveled, Dalhart, Texas.—Soil Conservation Service.

tions" are superior to contour furrows, and in maintaining cover, keeping out weeds, and hastening recovery, they possess even greater values.

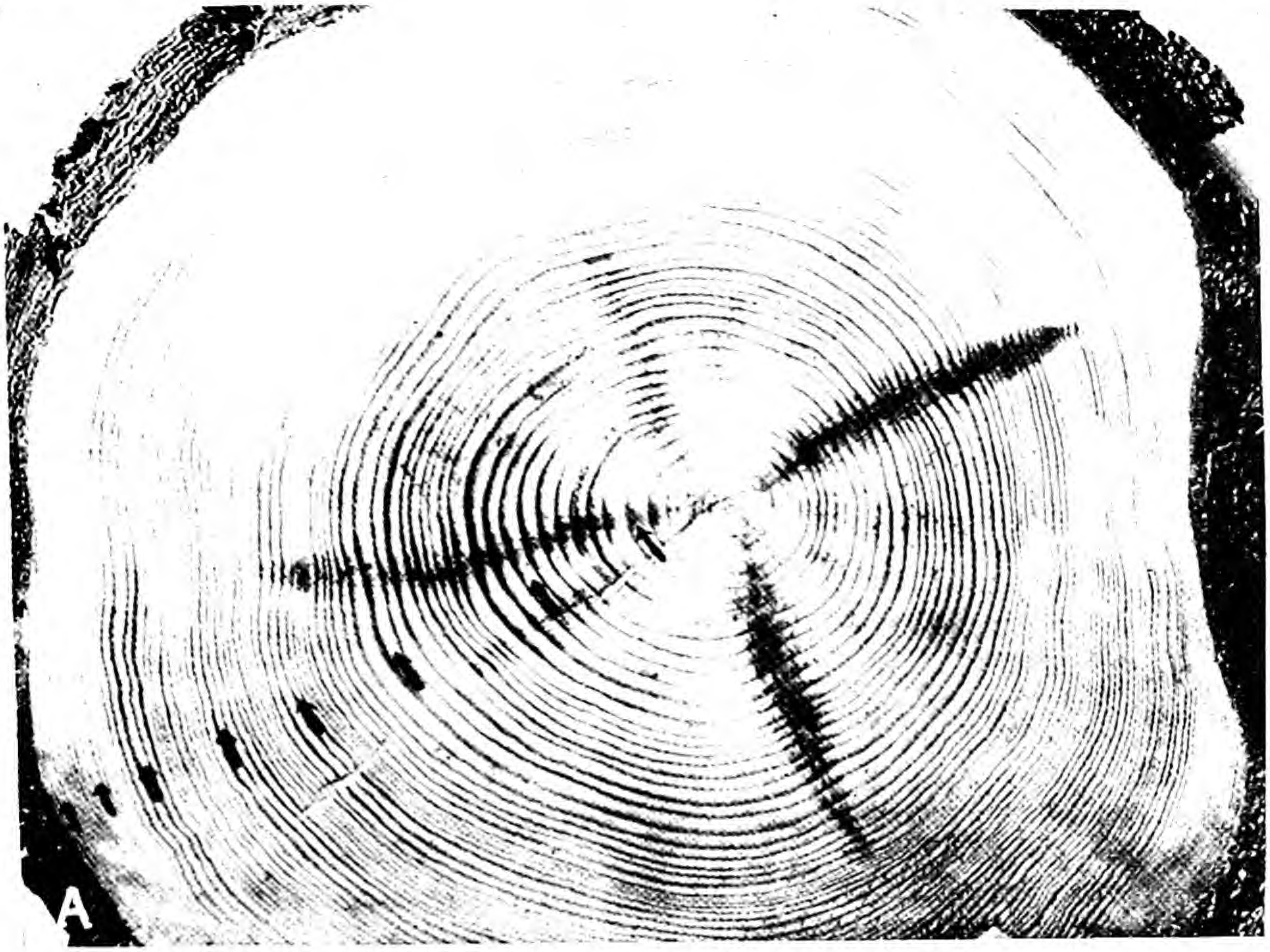
The study of the relation between cover and wind erosion has disclosed several facts of direct bearing upon the question of the formation of loess deposits. The current view is that the fine material was picked up by the wind during drouth in grassland and laid down several hundred miles to the eastward. This theory has been evoked to support the assumption that dust storms have occurred throughout the geological history of the Great Plains and that man in consequence has little responsibility for the recent ones. Through years of field work in the West, dust storms have never been observed to arise from areas with good cover, even during drouth periods. Moreover, measurements of the reduction of wind velocity by sparse covers of short grass render it improbable that dust storms could have come from anything but bare soil. Throughout the "Dust Bowl," the dune ridges have been derived from fields abandoned during drouth, and they no longer move when a fair cover is restored. These new facts as to wind erosion and loess deposits were tested in the course of a motor trip to classical loess horizons in Iowa with Dr. Kay and Professor Phillips. As a result, it was agreed that loess had not been derived from grassland but originated from wind erosion on bare glacial outwash plains and valley deposits (Plate 55).

Chapter VII

CLIMATIC CYCLES AND HUMAN POPULATIONS IN THE GREAT PLAINS

Early Records of Cycles.—Everyone is doubtless familiar with the account of a climatic cycle and its effects which appears in the Book of Genesis. The seven fat and the seven lean years suggest that this coincided with the well-known sunspot cycle, which usually ranges between 10 and 14 years. The seasons of rainfall and drouth, of plenty and famine, bear a close resemblance to recent periods of abundance and want. Accordingly, Joseph must receive the credit for issuing the first-known long-range forecasts of rainfall and drouth. He also achieved a world's record for verification, which has not yet been equalled in these modern times. Moreover, he was not only the first to propose but also the first to operate successfully an ever-normal granary. Another cycle—or rather, another expression of the same one—was mentioned by Bacon at the beginning of the seventeenth century, when he said that every 5 and 30 years in the Low Countries the same kind of weather is reported to come about again, such as great wet, great drouths, great frosts and warm winters, and that in computing backward he found some concurrence.

More than two centuries later, the Swiss geographer, Brückner, rediscovered the 35-year cycle, which came to be known by his name. He used all the long records of rainfall and temperature then available and was able to extend his study as far back as 1020 A.D. by employing known changes in level of the Caspian and other seas, the records of ice conditions and severe winters, and the dates of poor wine-grape harvests. He recognized 25 cycles between 1020 and 1890; though their average length was 35 years they varied from 20 to 50 years, which suggests that they too, perhaps, were multiples of the sunspot cycle. More recently, Douglass and Huntington have found similar cycles in the annual rings of trees, and the former has made brilliant use of them in dating prehistoric pueblos of the Southwest. He likewise has discovered evidence of dry and wet periods in the rings of fossil trees that flourished millions of years ago. Moreover, seasonal melting of the ice as the continental glaciers withdrew to the North at the close of the Glacial Period



A. The eleven-year sunspot cycle in the annual rings of a Scotch pine tree. (After Douglass, Carnegie Institution of Washington.)

B. Short grass cover of blue grama, buffalo grass and other grasses, seriously affected by overgrazing and drouth. "Dust Bowl," 1937. (U. S. Geol. Survey.)

produced characteristic annual layers in which Antevs has found cycles, and some 40,000,000 years ago similar deposits were being laid down in the Green River lakes of northeastern Utah and southwestern Wyoming (Plate 56A).

Wet and Dry Cycles in the "Short Grass" Plains.—Those who have traveled to the Rockies from the East have crossed the short grass country and have seen the low sod of grasses to which it owes its name. Since the days of trapper and pioneer, these have been known as buffalo grasses, not so much because bison preferred them as because the animals grazed off the taller grasses and left the shorter ones in their wake during spring and fall migrations. When cattle succeeded the bison and were held in herds or under fence, they grazed much more closely than the moving bison, keeping the plant cover in the short grass condition almost constantly. This effect was naturally greatest in dry or drouth years, so that the buffalo grasses logically appeared to be indicators of an arid climate. The first suggestion of this relation was made by Pound and Clements who explored the sandhills of Nebraska in 1892 and 1893, on the eve of a more devastating drouth than the West had known before that time (Plate 56B).

Almost everywhere, they found a close curly sod of buffalo and grama grasses, and they naturally concluded that this represented the normal forage crop of that particular climate—as it did for the time being. The tall grasses had not only suffered most from drouth itself, they also had been grazed so closely that they either seemed to be absent or at least to be unimportant. As a consequence, the opinion arose that short grass indicated a climate too dry for farming and adapted only to the cattle industry. This view became current among biologists and there was little occasion to doubt its accuracy before the exceptionally wet summers of 1914-15, when tall grasses seemed to spring up by magic. Relicts of the original grassland have since been discovered in all sorts of protected locations, the most interesting and best dated being the cemeteries of frontier towns, while the most widespread and extensive are the fenced right-of-ways of railroads (Plates 45 and 46).

Exploration during the two decades following has proved that taller and shorter grasses live together where the former have not been destroyed by grazing. To make the proof conclusive, small areas of a few acres each were fenced off as early as 1918 in various parts of the West, in co-operation with the Forest Service, Biological Survey and state experiment

A. Climax prairie of mid and short grasses in eastern Wyoming, in 1870. (Photograph by W. H. Jackson, U. S. Geological Survey.)

B. Blue grama on native pasture during period of seed dissemination. Clements, Texas. (Soil Conservation Service.)

stations. The desired evidence promptly appeared in the form of mixed prairie, so-called because a layer of mid grass developed above the short grass sod and reduced both grama and buffalo grasses to a secondary role. The narratives of early explorers and forty-niners furnish further proof that the original plains vegetation was mixed. However, the most decisive testimony has come from photographs taken by the Hayden geological expeditions in the Great Plains between 1867 and 1870. These pictures depict an undisturbed landscape with a luxuriant cover of tall wheat, spear and blue grasses, beneath which their shorter companions are completely hidden. The omnipresent sagebrush of later days, which has spread widely because of overgrazing and recurrent drouth, is nowhere to be seen (Plate 57A).

However, in scientific matters as with the daily press, correction is often slow to overtake the original fallacy. On the ground, short grass seems convincing and any one who sees it can understand why the view that it is a trustworthy indicator of climate and crops still persists in some quarters. Recommendations for the removal of a large part of our western population have been based upon the assumption that short grass is the natural vegetation of the Great Plains, that this proves the region to be unfitted for crops and that a great reduction in population therefore is imperative. On the contrary, we know beyond question that short grass is a man-made cover, and we are confident that rain and drouth will continue to follow each other as they have done in the past centuries (Plate 57B).

Migrations into the Great Plains.—The first homestead act, of 1862, stimulated thousands of men released from military service to test their fortunes in the fertile prairie soils of eastern Nebraska and Kansas. A few years later they met the turn of the cycle in the disillusioning drouth period of the early seventies, and this misfortune was rendered all the more tragic by the most devastating plague of grasshoppers known in America. These adverse conditions partly checked the wave of migration, but a favorable shift of the cycle for the next 10 years inspired the greatest inrush of settlers known in the peopling of the West. With memories of grasshopper years in mind, pioneer and newcomer alike felt that drouth and hard times had passed for good and that the future held nothing but timely rains and bountiful crops. This feeling was capitalized by those with lands to sell or commonwealths to build, and in good faith even men of science gave their support to the myth that the

climate had permanently changed for the better as a result of settlement and cultivation. Such beliefs were disturbed by the drouth of 1889 and shattered for a generation by that of 1893-95, when the exodus from the parched regions sent a half million settlers across the Missouri and back to their homes in the East.

The passing of the drouth years found a new generation of home-seekers pressing into the Great Plains after two periods of unusual rainfall, the first lasting from 1905 to 1909 and the second from 1914 to 1916. This later migration was intensified by the wartime demand for wheat, and the severe drouth of 1917-19 went almost unheeded amid fabulous prices for grain. A dry year now and then passed with scant notice until the collapse of the world market for wheat produced chronic agricultural depression, which became acute with the crash of 1929 and the onset of general drouth a year or two later. Today, many persons believe that the last seven lean years have been a period of all but complete failure of both rain and crops. We shall see that this picture is not generally true, even for the most arid districts. Drouth is always front-page news, a local dust-storm wears seven-league boots and a true sense of proportion can be secured only by wide perspective extending through decades.

Sunspot Cycles and Annual Rainfall.—We customarily think that the rainfall of a special year shows a fairly uniform pattern of amount and distribution in any selected region. It actually may vary widely, much as it does in a single storm. Almost everyone, in these times of fast motor-cars, has had the experience of driving out of one storm and into another. One may also drive from areas where rains have been plentiful to nearby places, where they have been scanty. Close uniformity in terms of well-known regional tendencies is reached only during the driest or wettest years, and even these may show local variations. Nevertheless, precipitation is not normally a hit-or-miss affair, for the very nature of forest, prairie and desert demonstrates that rainfall patterns are distinct. No two neighboring localities in the same region can maintain a material difference over a number of years without differing in their characteristic or climax vegetation.

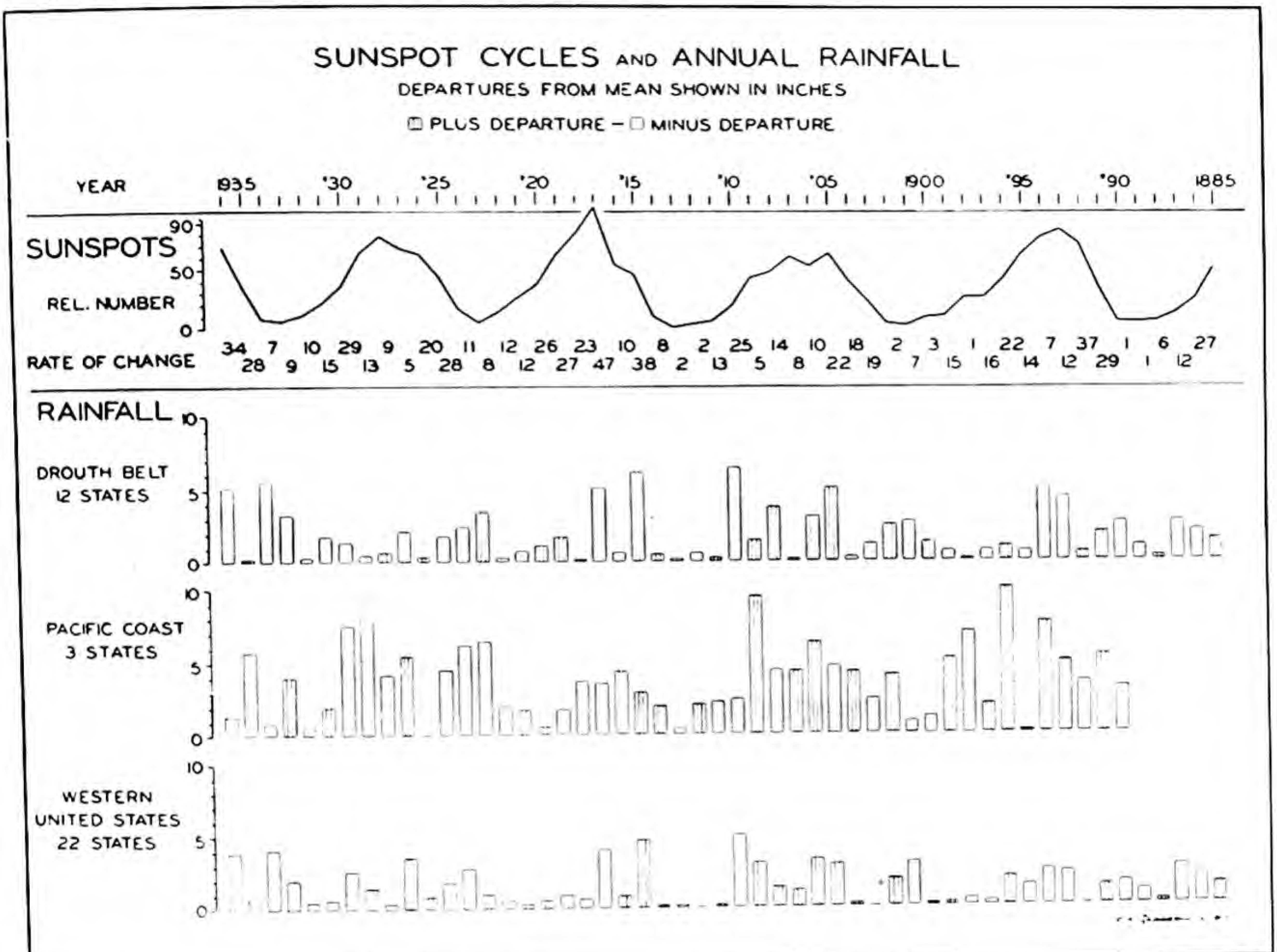
In seeking to explain the alternation of dry and rainy phases within cycles and the chain of consequences that lead to shifting populations, we may logically turn to fluctuations of the sun as the earth's source of energy. Such attempts have been made with increasing frequency since

1868. Most of these inquiries have found some agreement between dry or wet periods and the variations in solar radiation which are indicated by the number of sunspots; in some studies at least, the correspondence is striking. In the hope of discovering a connection between drouth and sunspot extremes, the rainfall records of all stations in the Middle and Far West were compiled in 1921. The first result of this study was the discovery that the three greatest drouths coincided with the greatest sunspot maxima (of 1870-72, 1893-95 and 1917-19), when the number of sunspots for each of the three maximal years averaged 85 or more. The alternate maxima of 1883 and 1905 were marked by a relatively low number of 63 spots, and rains were generally good to excellent in and about these years. Tentative forecasts of a maximum of about 100 spots in 1917, attended by serious drouth, and of approximately 75 spots in 1928, with normal rainfall, were verified.

Through the cooperation of the Works Progress Administration and the Forest Service, rainfall records have been compiled in terms of excess and deficit (contrasted with the mean amount) for the whole North American continent. The first fruit of this project is a table of state averages and their annual departure from the mean, beginning with 1876. This table confirms the occurrence of drouths at high sunspot maxima and it also reveals a marked tendency to drouth years at times when the spots are fewest. Furthermore, it not only corroborates the trend toward normal precipitation at the low maxima of 1883, 1905, and 1928, but also discloses that normal rainfall or better occurs between sunspot extremes. The following graph, based upon this table, does not include the drouth of 1870, but it shows that two great drouths fell at the high maximum of 1893 and 1917, while similar deficiencies occurred at the five minima between 1890 and 1933. However, this leaves unexplained the dry years of 1886-87, 1910, 1925 and 1930-31. Their cause is suggested by the fact that each coincides with an abrupt change of 25 to 30 sunspots in the direction of either maximum or minimum.

The periods of good rains from 1875 to 1928 have been 1875-78, 1881-85, 1902-09, 1914-15, 1920-23 and 1926-28, with frequent single years intervening. Beginning with 1929, the departure from normal in the West generally and in the drouth-belt in particular has been uniformly minus, although the deficit was slight in 1929, 1932 and 1935. The dry period of 1929-36 is the most nearly continuous that has been recorded for the United States, but the interval of 1893-1901 was virtually as

severe. Bad as it has been, the severity of the drouth of 1934-35 has been much overestimated, largely because of dramatic dust-storms. This reassuring opinion is supported by a consideration of the potential crop-yields between 1928-1938.



Sunspot cycles and annual rainfall in the western United States in relation to sunspot maxima and minima and rate of change in numbers from year to year.

Influence of Drouth on Plants and Animals.—In a state of nature, probably no living thing escapes the ravages of drouth in some form or degree. The effects are felt first by plants and especially by annuals, whose fate depends upon a single season. The great crops of the western world—corn, wheat and other small grains, cotton and sorghums—are annuals, most of which are subject to the whims of a hot summer, when a few days may do irreparable damage. Nature's crops, with the exception of weeds, are largely perennial; this is especially true of plants that make up the great vegetations or climaxes. It is practically impossible

for a drouth of several years to do more than stunt them, unless man has complicated the situation. Most insects, as well as many other animals, live as adults during a single season, and resemble annual plants in being highly responsive to drouth. Those of longer life-span, such as birds and mammals, respond more slowly and their numbers fluctuate to correspond, rising or falling during cycles of several years. In the case of grasshoppers or locusts and certain rodents, periodic increase is often so great that it produces veritable plagues, like those which marked the grasshopper years of the seventies. Grasshopper plagues in the West seem to be direct results of migration caused by drouth; this relationship apparently has existed in Europe and the Orient since Biblical days. Between the time of Charlemagne and 1862, the migratory locust invaded Europe 132 times, and 122 of those invasions were devastating plagues of the first order.

In the far North, the periodic shifts in the populations of snowshoe rabbits or hares are of tragic importance to Indian tribes and to such predators as the lynx, fox and marten, whose basic food is rabbit meat. These variations are the best documented of all animal cycles, since an exact record of the fur trade has been kept by the Hudson Bay Company for more than 100 years. Seton has shown graphically the fluctuations in rabbit numbers and the corresponding rise and fall in the number of the snowshoe's chief enemies. These variations corresponded closely. There also is general agreement between times of maximal numbers and sunspot minima, probably because there is greater warmth and better plant growth at such periods.

The last act in the full cycle of climate is the movement of human populations. This, in itself, is a cycle of advance and retreat. There have been four chief occasions for such tide-like movements in the West, in which the advance was timed by superior rainfall and good crops, while backward movement matched drouth and crop failure. The first two crises fell in the early seventies and nineties, at times of high sunspot maxima; the third came at the maximum of 1917 during war-time, with its high markets and greatly reduced man-power, and it consequently received little notice. The fourth and last occurred in the midst of depression, when the machinery of relief already was in action, so that the usual mass movement eastward did not materialize. That the question of enforced depopulation is a critical one is shown by the attitude of the Great Plains Committee. In August, 1936, it expressed the opinion that

the region could sustain its existing population; a few months later, it wondered whether reduction in numbers might be imperative. Its final conclusion, which appeared early in 1937, will receive consideration later.

Meanwhile, a nation-wide study of economic conditions, entitled "Migration and Economic Opportunity," has been published, the view set forth in this report being: "In the case of the Great Plains the minimum exodus consistent with the safe use of the land would be a quarter of a million people and the ideal economy would require the removal of nearly three times as many. . . . It is our judgment that the long-run direction of movement must be toward the urban areas and hence there cannot fail to be large movements from agriculture into other occupations." The report goes on to consider what these occupations are and the possibilities of jobs in them. After canvassing the national situation, it rather obviously indicates that there is only one other occupation for the 750,000 people to be moved out of the Great Plains, and that is work-relief.

Soil Erosion and Control.—Dust-storms, soil-drift and floods from 1933 to 1938 have made such a convincing case against man's handling of the soil that the verdict is unanimous and the task is now to carry it promptly and fully into effect. This is being done with increasing success throughout the Great Plains by the Soil Conservation Service, and the task of the ecologist as a student of environment is chiefly to analyze the role of vegetation in the processes of protection and recovery, in order to obtain a properly balanced control for the future.

There is nothing mysterious about the way in which plants act to hold particles of soil in place, but the combinations of different plant covers, soil, climatic conditions and human disturbances are innumerable. As a result, a matter which is simple in its essentials may become complex in practice. Moreover, vegetation not only protects the soil upon which it grows, but it also exerts a beneficial action for considerable distances beyond. This is easily seen in the case of windbreaks and shelterbelts, and it applies equally though less conspicuously to crops grown in strips and even to individual clumps of grasses. In all cases, plants slacken the movement of wind or water and reduce or even destroy their power to move loose particles of soil.

This ability to protect soil varies much with the kind of plant and the form of its stems and roots. Tall stems and dense tops make trees

the first choice for wind-breaks; shrubs and bushes rank next, while grasses and forbs come last. However, when we turn to the control of soil beneath them, grasses move up to parity with trees. The native mantle of grasses, tall or short, forms an all but perfect control of erosion by wind or water and continues to hold the soil against the force of the wind until nine-tenths or more of the surface is exposed by overgrazing.

Dead grasses may protect the soil almost as well as living ones, and they perform great service during dry periods before and after the growing season. Stubble gives comparable protection to grain-fields after harvest and permits methods of control in which seed is drilled into the ground without plowing. Stubble may also be saved as a litter which prevents blowing—but not in fields which are summer-fallowed. Since drilling reduces crop-yields greatly, strip-cropping probably is the best compromise between high yields and destructive drifting of soil.

Grasses and grains (which belong to the grass family) have one further advantage. Their greatly branched roots hold the upper layer of soil so firmly that particles often can be removed only with a power-stream. Since comparable agents are rare in nature, these roots give unusually strong protection against soil removal by either flowing water or wind.

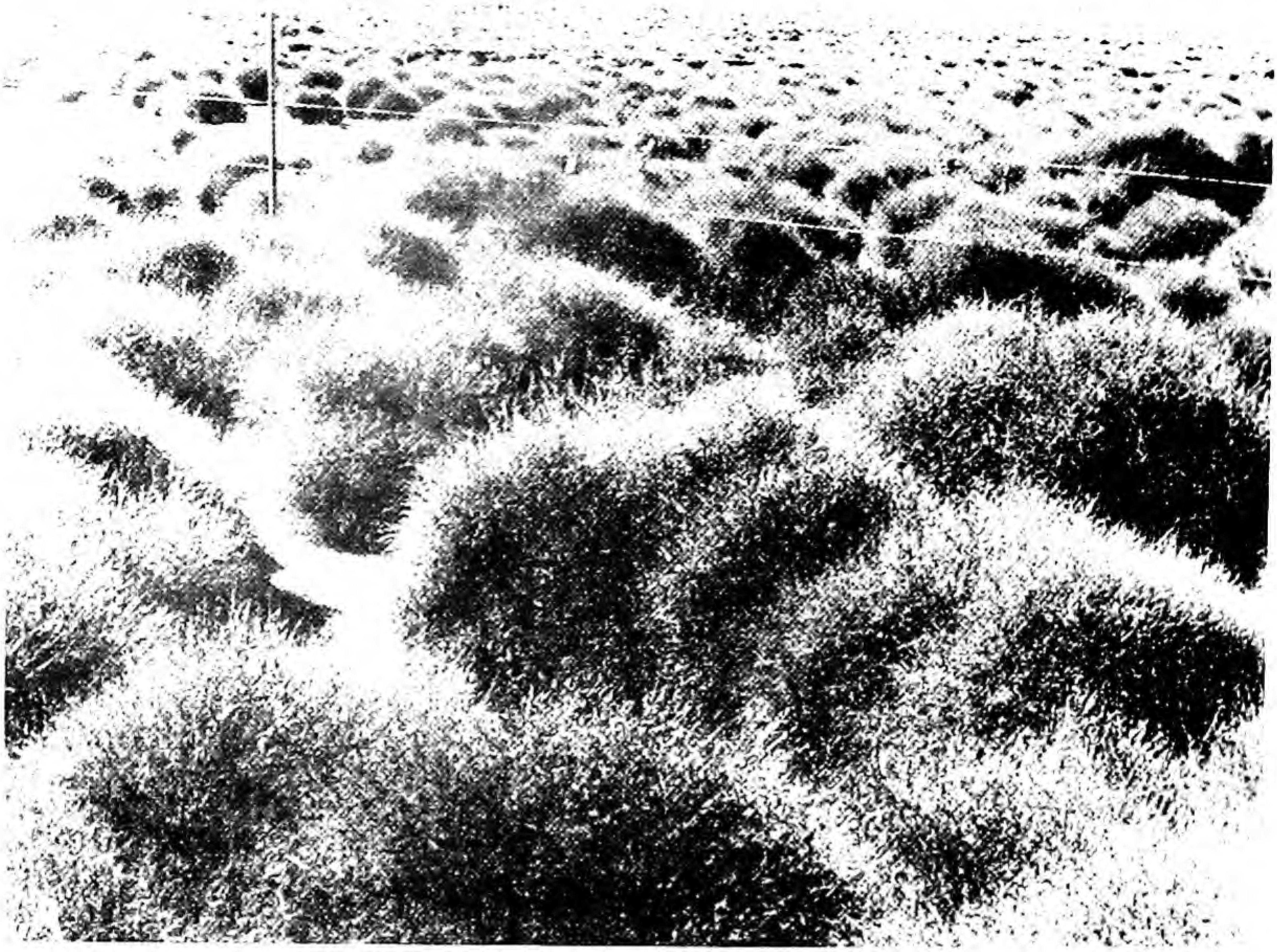
Grasses of the Great Plains take two familiar forms, known as *sod* and *bunch*. Bunch grasses are the more numerous, for their habits fit the prevailing dry climate. They usually are much taller than the sod grasses and have larger, denser root systems, but they cover the ground less uniformly than do the sod-formers. This latter group includes such outstanding types as wheatgrass, buffalo grass, and one or two of the grama grasses—if they grow under favorable conditions. Their stems are spaced closely and uniformly; all but wheatgrass are short grasses whose leaves form a more or less dense mat. They spread readily by means of rootstocks in the soil and runners upon the surface. Thanks to this ability, they surpass other plains grasses in ability to resist overgrazing and other disturbances.

Grasses also are divided into tall, medium (or mid) and short groups, according to their comparative heights. Stature corresponds closely to growing conditions and especially to available water. The three groups therefore reflect both the amount of moisture in the soil and the rain that falls upon it. Tall grasses, such as bluestem and sandgrass, require much water and hence occupy valleys or sandhills; the mid

grasses generally prefer sandy loams with less available water; and such short grasses as grama, buffalo and wheatgrass select the fine soils of the so-called hard-lands. When uncovered, the degree to which these soils will blow is determined chiefly by their texture and the amount of organic matter and water in them. Sandhills shift about constantly when they are exposed; the others drift less and less as their sand content decreases. It is an interesting correlation that sand, which blows most readily, is covered by the tallest grasses, the intermediate soils chiefly by mid grasses and the fine, compact silts by buffalo grass. However, the protective values of these three types are much more alike than their stature seems to indicate. Under natural conditions any one of them affords an almost perfect control against the strongest winds.

To appreciate how effectively grasses and weeds protect the soil surface, we need only to notice that they form miniature windbreaks. In this role, they reduce the wind velocity for a distance to the leeward that may be as much as 20 times their height. This is several times the distance between bunches of tall grass and the same relationship holds among the short grasses, which stand much more closely. Even a very open cover of native grasses will prevent wind erosion: a fact that is readily confirmed when we measure the effects of different grasses upon high wind velocities. Wheatgrass completely stills a wind of approximately 18 miles an hour at three inches above the ground level, while short grasses decrease it 20 to 25 times.

When vegetation catches and holds soil particles, it keeps the wind from picking them up to form soil-drift or dust-storms. Soil-drift means deposition, which builds dunes on farmlands as well as along sea-coasts and river-valleys; if uncontrolled, it buries windbreaks and fences and overwhelms farm buildings. Obviously, the best method of control is to prevent wind erosion, but until this is achieved generally, deposition must be brought about where it will do the least harm. Windbreaks, therefore, must be planted far enough to the windward of homes so that silt is caught and dropped before it reaches farmyards, or an outer low windbreak may be used to catch soil before it piles about the windbreak proper. Russian thistle and other tumble-weeds are especially undesirable because they come to rest along fences and windbreaks and thus produce deep drifts. Such tumble-weeds can thrive, however, only in soil that is cultivated or otherwise disturbed. A pasture strip to the windward of buildings will almost always eliminate danger from them (Plate 58A).



A. [illegible] B. [illegible] Russian thistle [illegible] South Dakota.

Some writers believe that dust-storms have occurred commonly throughout the later geological past and that deposits hundreds and even thousands of feet thick were produced by wind action. Without presenting the ecological evidence in detail, we may say that even a thin cover of vegetation controls the wind so effectively that soil-drift and deposition during the past must have been limited to bare areas such as ocean-strands and river-banks. During the historical period, dust-storms have come only from soils exposed by man in the course of settlement.

Of all the forces that act upon plant cover to destroy its protective power, those released by man are by far the most potent. The only natural one of great significance and wide extent is drouth, though floods and animals may exert much local effect. Even drouth is chiefly contributory and the train of events which lead to soil-drift and dust-storms is regularly set in motion by disturbances due to man. All these—cultivation, fire, grazing, road-building, etc.—lay the land surface bare and provide opportunity for erosion.

The control of wind or water erosion must be accomplished for the most part by means of vegetation; all other aids are merely contributory or are to be employed when the protective effect of plants is absent or while plants are being restored. Wind is more readily controlled than is water, since even an open cover does this effectively, not only beneath it but for considerable distance to the leeward. For the nearly complete control of runoff and erosion, a dense cover is necessary. Where cultivation of fields keeps such cover from growing, terraces, dikes and furrows must be used as reinforcements to plants. On the Great Plains, similar aids should be utilized where overgrazing has become a menace during drouth and renewed rains will bring volumes of water that the impoverished pastures cannot retain until it is absorbed (Plate 58B).

Reclamation of Ruined Land.—So thorough is the control exercised by native grassland that the return of croplands to grass in the Great Plains has come to be generally regarded as the proper, if not the sole, solution of the problems brought in the train of drouth and abandonment of crops. This belief, however, has failed to take into account several critical considerations, namely, that drouth itself, though recurrent, is always transient, that methods of proper cropping and erosion control have been developed and are being applied with increasing success, and that restoration of grass-cover involves much more than the mere broadcasting of seed over a landscape.

For two generations, attempts have been made to rejuvenate overgrazed and wornout ranges by the simple device of sowing seed and leaving the rest to nature. Such efforts have been uniform failures except under moisture conditions that rarely occur. As a consequence, we have been forced to look more closely into nature's ways in order to discover how she succeeds in improving pastures and re-covering abandoned fields when given the opportunity. With these facts in hand, we are able to speed up natural processes, to use other or better plants than those now available and to broaden the field of action. More than this, we can press into service some of the practices of cultivation and can secure combined forage and protection values resembling those found in fields of perennial crops. In such cases, the problem is narrowed to finding and maintaining the best grass crop and, of course, to secure the manpower or money needed to do this work.

When does grazing become overgrazing? The best answer is that this happens when weeds begin to increase in numbers at the expense of grasses. Since both compete keenly for a limited water-supply, anything more than moderate grazing throws the balance in favor of the weeds. The grass then decreases in amount, but since it is still called upon to support the same number of cattle, it suffers further handicap in its struggle with the weeds. Each step in the destruction of the forage cover is marked by the appearance of other weeds, until these competitors become masters of the situation. The grazing capacity of the land may be reduced to a half or a third and its protection against water erosion and flooding may be cut even more. So characteristic are weeds as indicators of the successive stages of deterioration that the forage production and protection value of a particular range may be estimated from the kinds and abundance of the weeds in it. When drouth comes, the remaining grasses have less water for growth, competition is intensified and the demands of cattle are relatively increased. The result is that the grass cover loses ground at an accelerated rate until (to the unpracticed eye) its ruin seems complete. But fortunately, while grass may be eaten down to the roots, it is rarely if ever eaten out, but persists and is ready to renew growth under more favorable conditions (Plate 59A).

The best cure for the ills of overgrazing is to be found in the natural recuperative power of grasses and the chief task is to afford them a fair opportunity. Natural recovery is so much more automatic and economical than restoration by sowing or planting that it should always be given

an adequate test before artificial methods are used. The essential requirement is a resting spell in which the grasses may make and store food for growth; this demands a reduced number of grazing animals per acre. Complete removal of cattle for a year or two is often desirable, but too frequently it is impossible, especially during drouth. Instead, herds must rotate from pasture to pasture or grazing must stop during a special period. Since grasses are most susceptible to damage when they are becoming green in the spring, spring grazing generally should be deferred as much as possible. Delayed grazing demands an adequate supply of fodder, a fact that makes the general development of forage crops an indispensable feature of any successful farm system for the Great Plains.

The question of how far artificial re-grassing is desirable must remain open until the method has been tried in the various climates and covers and the cost of assured results is determined. However, where erosion is active and the flood risk to large cities is great—as it is on the divide between the Platte and the Arkansas rivers—the cost of restoring an effective cover is much less important than the speed with which it can be done. In all such areas sowing and planting should be used to hasten recovery as much as possible. Unfortunately, two of the best species for this purpose, buffalo and wheatgrass, are not well adapted to this region, while a moderate reduction in stock for a year or two and regulated grazing thereafter probably would remove flood danger to cities along the mountain front. These measures must be reinforced by terraces, check dams and reservoirs to provide assurance against the occasional torrential rains which are popularly known as cloudbursts.

Recovery in Abandoned Fields.—Each receding wave of population on the plains has left in its wake thousands of abandoned fields whose management has reverted to nature. She has taken these areas in hand and in her own deliberate fashion has called in a succession of plant communities to re-establish the grass cover, beginning with weeds the first year. In some instances this restoration of grass was a relatively simple matter; in others it was exceedingly difficult. Deep-seated disturbance, lack of a proper supply of seeds and recurring dry years hampered progress. Worst of all, such fields frequently were too quickly returned to grazing—often in the first weed stage or even by utilization of the abandoned crop. In consequence, large areas of the Great Plains are checker-boards of abandoned fields in all stages and degrees of re-

A. Climax mixed prairie in eastern Colorado, reduced by drouth and overgrazing to short grass which has been finally replaced by prickly pear.

B. A "suit-case farmer's" abandoned field, reclothed within five years

covery. They can be fashioned into a nicely graduated scale for the study of regeneration and utilization.

For hundreds of these fields in various districts, Savage, Judd and other workers have been able to determine the year of first or renewed cultivation, the number of years under cropping, and the date of abandonment, which determines the length of the period during which succession has acted to bring about natural recovery. The most significant discovery in this connection is that succession operates most rapidly in fields of the "suitcase-farmer," usually a city dweller who leaves his desk or bench to sow a crop and return later to harvest it. He embodies all the undesirable practices in cropping, plowing his field sketchily at the outset and drilling the wheat in each year without further cultivation. His methods are poor, but he does not destroy the underground perennial parts of the native grasses, which may survive as many as 16 successive crops and still be ready to reclothe the soil effectively in three to five years. Fields in sandy soils or sandhills likewise permit rapid succession and again become covered with characteristic stands of tall bunch grasses in about eight to ten years. If land values warranted it, artificial aid would doubtless hasten the process (Plate 59B).

The situation is quite different in the finer soils of the so-called "hard lands" where cultivation has been more thorough, usually to the extent of some ploughing for each crop. Rootstocks may survive for two or three years, but in the great majority of the fields that have been abandoned four years or more, succession depends upon seeds and hence proceeds very slowly. It is possible that some seeds remain alive in the soil for several years, but as a rule they must be blown in from adjacent areas where grazing is moderate or absent and grasses are able to produce seed. Roadsides, railways and other protected areas furnish the chief supply, especially where they lie in the direction of the prevailing wind. But under such conditions the ground is largely bare at 8 to 10 years and still about half exposed at 18 to 20 years, while the normal cover is usually restored only after 30 to 40 years. Obviously this is far too slow, even if grazing can be excluded, and recently abandoned fields of this type can be promptly returned to grass only by artificial methods, such as sodding with buffalo grass. Fortunately, the great majority of existing fields are now well along in the process of natural succession. Some will require no aid and others a relatively small amount, while those withdrawn from cultivation during the past 5 years will need com-

plete artificial treatment, where it is deemed best not to return them to crop production.

Crop Production in the Great Plains.—The ecologist looks upon grassland in general and the prairies and plains in particular as almost inexhaustible reservoirs of soil fertility—of the raw mineral materials which are essential not merely to plant growth but especially to high yields. It was not by chance that grasslands of the Mississippi and Missouri valleys became the scene of the greatest corn and wheat production in the world. There were many reasons for this, but the most significant were depth of soil, abundance of available humus and materials, presence of lime, readiness of nitrification, and number and abundance of nitrogen-fixing plants. Virtually the only limiting factor was water, whose amount was restricted by rainfall which decreased progressively to the westward, and by recurrent periods of drouth. Under these conditions the advantages of wheat, especially winter wheat, soon were recognized and this grain came to be the major and too often the sole crop of the region. In spite of drouth, sagging markets and justification for an expanding grazing economy, wheat continues to hold its preeminent position.

The point to be emphasized is that under proper tillage wheat has produced a fair and often a large return for a quarter of a century throughout most of the Great Plains. Where it has failed more or less completely in large areas, failure has also swept across much of the subhumid Missouri Valley. In spite of its greater requirements and longer period of exposure to the vicissitudes of summer, corn also has been a profitable crop, especially when the value of forage or stover is considered. This is even truer for the grain sorghums such as milo and kafir.

The most significant fact for the solution of the population problem in the Great Plains is to be found in the yields of grain, and especially of wheat, at the experiment stations of the Division of Dry Land Agriculture. Along the eastern line of stations from North Dakota to Oklahoma, average wheat yields for the decade ending with 1935 ranged from 17 to 31 bushels per acre. In the western series of stations, with a rainfall several inches less but with the same compensation of higher elevation, yields were practically the same: 17 to 30 bushels per acre.

With respect to balanced cropping and the feeding of stock, the average yield of corn was 20 to 22 bushels per acre, while milo ranged

from 23 to 34 and kafir from 21 to 25. The fodder as a rule approximated 2 tons per acre.

Yields on farms in these same regions were much lower. But no one conversant with the situation expects to save agriculture and the farm population in the Great Plains by a continuance of the practices that have brought about existing conditions on average farms. The Soil Conservation Service's achievement in winning the farmer's cooperation in conservation farming and in securing results far out of proportion to the brief period of its existence, shows that western agriculture can be, and is being, improved. Moreover, a direct and complete answer to the question is furnished by Charles Peacock's farm in eastern Colorado, where basin furrows are employed to retain all moisture that falls in a region whose yearly precipitation is about 16 inches. This device, coupled with a generally excellent system of tillage, has produced yields of 18 to 22 bushels of wheat per acre each year since 1932, with the exception of 1935. Failure in that year was due to grasshoppers, which took the winter wheat as fast as it appeared above ground in the fall of 1934. Since these farms enjoy no peculiar natural advantage, their crop-yields fully support the results achieved at the various dry-land stations. When the two sets of yields are combined, they leave little room for doubt as to the Great Plains' capacity for wheat production. In fact, the yields obtained during the decade of most serious drouth in our history compare most favorably with normal averages in the more humid districts several hundred miles eastward.

Long-range Weather Forecasting.—Almost everyone admits that a method of long-range forecasting as accurate as the daily predictions of the Weather Bureau would be one of the greatest conceivable boons to agriculture. The outstanding achievement in this field has been the prediction of monsoon rains, by means of which the threat of famine has been reduced in India. In this country, McEwen's October predictions of winter rainfall in southern California have been so successful that his researches have received financial support from utility companies interested in annual forecasts of hydro-electric power. During the 21 years of forecasting, he has obtained an agreement of 75 to 80 per cent between predicted and recorded rainfall. For southern California, McEwen made 15, and for the Santa Barbara region 17, successful forecasts during these 21 years.

The physical system in the interior of the continent is more complex

than that of the Pacific Slope and demands different methods. In the tentative effort to find a basis for prediction of rainfall in the Great Plains, solar radiation in terms of the sunspot cycle has been the chief reliance. This has been supplemented by correlation between the rainfall of this region and that of California where Santa Barbara is under test as a key station because of its intermediate position. This correlation has amounted to 70 per cent since 1896 and 80 per cent since 1923. It possesses a unique advantage for prediction year by year, since California rainfall precedes that of the growing season in the Middle West by 6 or 7 months.

The first attempt to anticipate major fluctuations in rainfall on the basis of the sunspot cycle was made in 1913 and was confirmed by a moist season. The second tentative forecast, made in 1916, anticipated the drouth of 1917 from the number of sunspots at the approaching maximum, while the third suggested fewer than 80 sunspots for the maximum of 1928, with generally good rainfall. The drouth year of 1930, which ushered in the recent dry period, was wholly unexpected, since the apparent significance of a rapid change in numbers of sunspots had not been perceived at that time. This new index suggests a plausible explanation of drouth in 1930-31, with a rate of change of 29, and in 1936 with one of 32 spots, while the sunspot minimum of 1933, which carried over into 1934, is thought to explain these dry years. The present course of the sunspot cycle indicates a high maximum in 1938, and the forecaster is torn between the desire to see the sunspot indexes again confirmed and the hope that good rains will temporarily contradict them.

Importance of Determining Soil Moisture.—In 1907 in connection with a classification and use survey of Minnesota, it was suggested that the farmer might well emulate the ecologist and carry a soil augur for measuring the amount of moisture in his fields. Hallstead has put this method to eminently practical account at the Hays Experiment Station; he has also shown that the farmer needs only a spade to learn the depth to which the soil is wet enough for plant growth. This depth at seeding time is closely related to the yield of wheat, a moisture layer of three feet in fairly heavy soil virtually insuring a good crop. With a shallow, wet layer, failure is frequent, and when dry weather occurs during autumn or winter, abandonment is often desirable.

The most significant outcome of the practice of testing soil moisture is that it permits an early and impersonal decision as to the advisability

of abondoning the growing crop and conserving water for the next one by means of fallow, which serves to keep down weeds. In short, it gives the farmers two chances for a good wheat yield, since fallow usually produces twice as much as continuous cropping. An important item is that moisture determinations render a fairly decisive judgment at a time when the farmer is still inclined to gamble on rain. With the water-content low and rainfall deficient to April first, abandonment of the crop and the use of summer fallow is strongly indicated. To harvest the wheat crop in good years and abandon it in poor ones gives the flexibility needed in a region where dry years are not rare and drouth periods are recurrent. It is a type of crop insurance that requires neither subsidy nor enormous granaries, and is peculiarly adapted to maintain the independence of the farmer while it stimulates his thinking processes.

A necessary adjunct to the combined method of anticipation and prediction is the adjustment of crops to seasonal differences in rainfall and soil moisture. In general, corn requires more water than winter wheat, wheat more than grain sorghum, which in turn uses still more than the various forage plants. The special needs and values of the different crops for the diverse regions of the Great Plains have been so thoroughly demonstrated by the various state and federal experiment stations that the information is necessary to every farmer. The prerequisite to its general use is advance information about the farmer's capital in terms of moisture. We have found that the most important forecast can be made by the spade, but it is not improbable that this can be reinforced and anticipated year after year by means of long-range indexes.

Population and Relief in the Great Plains.—When we turn to the related questions of population and relief in the Great Plains, two or three outstanding facts appear. The first is that in spite of a critical drouth period, unequalled in duration, the population of the 10 plains states has remained virtually stationary. Obviously, this stability has been greatly helped by relief and subsidy, but these factors were not peculiar to the Great Plains. Since the population maintained itself during this most tragic of times, there is little prospect, and no necessity, of transplanting it during better years. In a sense, the farmers and ranchers of the Great Plains are still pioneers, with characteristic hardihood and attachment to wide horizons together with mobility and independence. But they live on an economic and cultural level far above that of the hillbilly and share-cropper, and by comparison constitute a simple problem.

A. Dunes formed from soil blown in from ploughed fields during the drouth of 1934-5, being leveled by Soil Conservation methods; Dalhart, Texas.
B. Corn crop grown on the same land in 1937.

All the facts agree in demanding that their problem be solved in their own familiar environment.

The ecologist long familiar with the Great Plains entertained no doubt that this could be done. From the very outset, he hoped that the winds which had fashioned the drifting fields into dunes 30 feet high and a half-mile long, could be tamed and forced to blow them down again. This was done by the Soil Conservation Service, under the direction of C. J. Whitfield, and the area once thought to be ruined beyond redemption now grows crops of corn and sorghum on its flattened ridges (Plate 60).

The most serious defect in the past has not been that of climate, natural vegetation or potential crop production. It has been the common failure to realize that the price of continued use is conservation and that conservation can be secured only by means of the most thorough cooperation. First of all this must embrace all the official agencies, federal, state and county, in any way concerned with the problem; this unification has already been accomplished to a considerable degree. It has shown farmers the necessity of cooperation among themselves, and it is upon this new development that the conservation of tomorrow should build an enduring system of use without abuse.

These ecological considerations were brought to the attention of the Great Plains Committee shortly after its pessimistic statement of October, 1936, with the consequence that its final recommendations to the President were summarized in these words:

"In this task of realizing the true and lasting values of the Great Plains, the whole nation has more than a sentimental stake. The Great Plains can be made a source of a large portion of our food supply. Investments in their development can be secured from uncertainty, and under proper conditions new investments can be made securely. The Plains can be transformed from a risky adventure and a recurrent liability into a stable basis of economic and social profit to their inhabitants and the whole country."

Chapter VIII

ECOLOGY IN THE PUBLIC SERVICE

Review of Guiding Principles

Since its beginnings in the early part of the century, dynamic ecology has come into wider opportunities of service in such well-established fields as forestry, agronomy and grazing and has contributed steadily to the foundation of those more recently developed, such as erosion control and water supplies. With the present great expansion of federal projects has gone a corresponding increase in the utilization of ecological methods and concepts, even when this term has not been used. How widely the comprehension of the basic role of ecology in human affairs has spread may be seen from the statements of progressive thinkers in various fields. Professor Murchison takes both plant and animal ecology into account in his "Handbook of Social Psychology," H. G. Wells has said that "economics is a branch of ecology," and General Smuts stresses its significance in "Holism and Evolution." Elsewhere he has stated that "Ecology must have its way; ecological methods and outlook must find a place in human government as much as in the study of man, other animals, and plants. Ecology is for mankind."

The essence of ecology was long ago said to be measurement, experiment, development (dynamics) and synthesis (Clements 1905). It is obvious that much that bears the name of ecology possesses these qualities not at all or in small degree, as is also the fact that they may be present without the name. From its very synthetic nature, ecology is not to be regarded as a specialized field comparable to physiology or morphology or even zoology, botany or geology, but as a point of view and a plan of attack. As such, it justifies fully the statements quoted above and embraces all problems in which life and its environment are concerned. It is not only inclusive in comprising all the aspects of the cause-and-effect sequence in individual and community, but likewise in embracing all organisms from protophyte and protozoan to flowering plant and man. In this conception, no other term possesses the intrinsic significance of ecology, as none other denotes the unremitting search for causes.

Concepts

These have already been discussed in detail in the preceding chapters and in "Plant Succession" and "Plant Succession and Indicators,"

hence only the more salient principles will be recapitulated and emphasized here. The first of these is that the community is a complex organism of a wholly different order from the individual plant or animal, but nevertheless an organic entity with functions and structure. As a whole, it is not merely greater than the sum of its constituent species and individuals, but these in turn are something different in the community from what they are when detached from it. The universal or final control of all community life resides in the climate, in conformity with which the grand communities are termed climaxes, while the immediate control may lie in land-form, soil or some activity of that super-dominant, man. As a consequence of its response to these in varying degree, the climax exhibits a complex structure determined by its development, which in turn is an outcome of the functions of the community. These interact to constitute the growth and behavior pattern of communities of all degrees and of all kinds from the simplest family of unicellular organisms to the highly specialized societies of man. The mere enumeration of such functions suffices to show that they are universal in character and that most of them possess at least a general human connotation. The complete list comprises aggregation, migration, reaction, coaction, competition, cooperation, disoperation, ecesis, invasion, and succession, the last being an integration of all others and representing in the community the role taken by growth and development in the individual.

Reaction.—The driving forces in development or succession are to be found in coaction and reaction, the first comprising all the effects of the associated organisms upon each other and the second their modifying influence upon the factors of the habitat. All favorable coactions involve cooperation in some degree, while unfavorable ones give rise to disoperation of varying kinds, among which competition is of the first importance. In the reaction that marks each life-form stage or associes of a sere, cooperation is paramount at first and the resulting reaction consolidates the position of the community concerned. Continuing reaction leads to disoperation and competition with the consequence that the next stage enters and gradually takes possession, this alternation of effects persisting until the climax is reached, when cooperation with secondary competition maintains the characteristic stability. The initial investigation of plant competition has disclosed the details of the process for a number of life-forms, but a similar comprehensive and intimate study of reaction is yet to be made. It is obvious that reaction is universally the critical function

wherever the relations of community and soil are concerned, but this is nowhere so important as when the soil itself is to be conserved, as in the manifold types of erosion.

Coactions.—These embrace three different categories with respect to the organisms concerned, namely, interactions between plants, those between plants and animals, and those that concern animals directly or primarily. The last do not require consideration here, while the first have already been mentioned as involving chiefly cooperation and disoperation, competition being the chief form that the latter takes, though parasitism plays a subordinate part. The most significant coactions between plants and animals are those in which the latter take the active role as consumers of plants for food, often producing striking community effects. However, these are relatively insignificant in nature and rarely become considerable or controlling until man enters the situation by virtue of the various kinds of disturbances that he exerts.

As with the other animals, the coactions due to man are almost wholly a matter of destruction, direct or indirect, but he has a wider range of processes at his command and applies them on a much larger scale. Primitive man had at his disposal but the single tool, fire; the nomad added grazing, and the lake-dweller, clearing and cultivation. Construction for irrigation could hardly have antedated the historic period and the development of roads on a large engineering scale came very much later, as did draining and impounding in any considerable degree. In spite of the great variety of concrete coactions, all human types of disturbance may be summed up in those mentioned, and these are merely different ways of intentional or unintentional destruction. In short, man may be said to destroy to plant, and to plant to destroy, the chief exception being found in his growing tendency to check destruction by erosion control.

Succession.—Under primitive conditions, the great climaxes of the globe must have remained essentially intact, since fire from natural causes were undoubtedly both relatively infrequent and localized. Succession was far less general and was represented chiefly by priseres, especially in water and dune sand; subseres were few in number and small in extent. They became universal features only as man extended his dominion over nature through disturbance and destruction, and they are permanent today in the degree to which these forces are continuous or recurrent. From the very nature of climax and succession, development is immediately resumed when the disturbing cause ceases, and in this fact lies the

basic principle of all restoration or rehabilitation. Left undisturbed, every bare, seral or denuded area begins its slow but inevitable movement to the climax wherever the latter has not been destroyed over too large a territory to permit the mobilization of the successive populations.

As a consequence, it is only necessary for the ecologist to know the course and rate of each sere in order to control it or at least shape it to the desired purpose. The natural process once thoroughly understood, it becomes possible to retard or accelerate it, to "telescope" or hold it more or less definitely in one stage or to deflect it in any one of several possible directions, or finally to destroy it and allow the process to start again within the limitations set by the species available. Moreover, it may be manipulated as a sequence of natural communities, it may be modified by the insertion of introduced or cultivated species, or once so modified, it may again be restored to its proper development in the climax. As the final stage of a sere, the climax is less flexible in terms of manipulation, but it is capable of similar control; it can be protected and held against all but climatic change, as in research and wilderness areas. It can be enriched or impoverished, and it can be destroyed in such a way as to reproduce itself or so completely as to render this impossible, thus permitting a wide range of substitutions within the limits of climate and soil. In short, as an instrument for the control of the entire range of human uses of vegetation and the land, succession is wholly unrivalled.

Experimental Succession.—It is well understood that the body of knowledge concerning succession and climax has been built up chiefly by the method of comparative observation, though much of this has been directed to the quasi-experiments so abundant in nature, as well as those unintentionally set up by man. A direct experimental attack upon succession by any one individual has been discouraged by the length of time embodied in a single prisere, to say nothing of the expense and territory involved. Even the much shorter span of most subseres has been too long for the individual investigator as a rule, and no adequately quantitative and complete study has yet been made, though some may approximate this goal (1910).

From the foregoing, it is evident that great national projects that promise a lengthy or indefinite period for their realization constitute an opportunity for experimental succession that may never come again. Consequently, dynamic ecologists are justified in feeling that the time and energy spent on such problems will bring a double return. The im-

mediate and larger reward must spring from the service that ecological concepts and methods alone can render, but along with this is the chance to carry out experiments in vegetation on a scale and for a period never before possible. These are in essence basic social-economic studies that deal not merely with the setting, behavior and welfare of human communities, but also exemplify the great ecological processes that constitute society and foreshadow the control that man must achieve of such opposed community functions as cooperation and disoperation.

METHODS

These chiefly concern the community, though standard phytometers regularly consist of individual plants and indicator values rest upon the response and reaction of the species-individual or specient. The immediate objectives are the dynamics of plant and community as expressed in functions and processes, which are summed up in development as integration or growth and structure as the final outcome. Development in turn comprises the life history or ontogeny of specient and climax, and their evolution or phylogeny. As to procedure, investigation necessarily advances by analysis, with the realization that this is important in the understanding of the simple or complex organism only in so far as it contributes to synthesis. Indeed, there cannot be too much emphasis upon the statement that ecology has the synthesis of cause-and-effect relations of organisms as its one great goal. This is obviously as true of the habitat as it is of species or community and it applies with all the more force to the biotic community or biome, with man as the super-dominant.

While complete objectivity is the supreme goal of all science, it is even more essential to ecology in view of its inclusive nature. It can be secured only by the rigorous methods of physics and chemistry, but the obstacles to applying these to life and its setting may sometimes appear insuperable. Thus, in the case of such a basic factor as light, physical methods still leave much to be desired, while the accurate determination of response by the whole organism to it is at present impossible, at least outside of an aqueous system. In spite of this, measurement and experiment by means of constantly improving methods and instruments constitute the distinguishing mark of dynamic ecology and afford the sole procedure by which it may gradually achieve much of the objectivity of physics and chemistry. As with these, interpretation and hypoth-

esis must always play a legitimate role, but primarily for the sake of guiding further experimentation, which in all instances must be considered the final arbiter.

Measurement in the broadest sense of the word is indispensable through the whole field, whether it involves the physical factors of the ece as causes or the responses of plant or community under existing conditions or subject to varying degrees of control. It is even more intrinsic to experiment, which becomes objective in nature only as it is quantitative in method. The immediate purpose of experiment is analysis of complexes, in terms of functions and processes, for which it is imperative to take into account natural conditions so-called, partial control of one or more factors and functions in field and garden, and complete control within the limits of laboratory technique. As has been emphasized elsewhere, the out-of-doors lends itself with difficulty to control experiments, while the laboratory is unsatisfactory in not permitting the use of complete organisms in the normal factor complex. In consequence, both must be utilized in the proper degree of coordination and preferably by the same group of experimenters, which often demands cooperation. As to the community, laboratory control is out of the question for the most part, but close approximations may be attained in greenhouse and garden in the form of miniature replicas.

Phytometers and Instruments.—It has become increasingly evident that the analysis of habitats by means of physical instruments alone is far from complete, partly because of the inadequacy of most instruments but chiefly because of the necessity for expressing physical and chemical measures in terms of plant functions. This is possible only by means of the varied control afforded by phytometers (1924), which must be assigned prior rights in all such studies, while instruments, though indispensable, must be relegated to a secondary position. Quite apart from their unique value in rendering the judgment of organism or community upon factor or complex, they also disclose the nature and degree of response and give a significance to physical units that cannot otherwise be secured. For single factors, community phytometers are often desirable and these may range from sod cores and sown and planted quadrats to closures of several sorts.

Quadrats and Closures.—Since the proposal of a comprehensive system in 1905, quadrats and transects in a variety of forms have become the customary procedure in all quantitative studies of vegetation (1929).

They have been extended and modified for special purposes, and the method of charting improved in accuracy and speed, first by means of the pantograph and then by using the overhead camera. The latter is definitely indicated in all communities where stature and layering are not too great, or even in some of these when combined with the bisect. List or census quadrats have little or no value in dynamic ecology by comparison with the permanent type, which are conveniently grouped as cut or clip, denuded and process quadrats. The first are designed to measure yield, the second to trace succession, and the third to follow and evaluate disturbance processes in particular. By contrast with surface relations, those of depth are determined by means of the bisect or better still by the bisect-quadrat.

The usual type of closure is the exclosure, a fenced area of suitable size which provides protection against the coactions of one or more groups or species of animal. The enclosure is similar in design, but is used to restrict animals to a definite area to permit the direct study of their influence, while the isolation transect is a combination of small units opened and closed respectively each year (1920, 1928). As a rule, exclosures are a few acres in extent and consist of two units, one fenced to exclude cattle and the other, larger rodents as well. Because of the protection afforded, they serve also for the installation of process series, which permit analyzing the effect of the various processes in disturbance and recovery (Plate 63).

Changes over an area larger than those recorded by quadrats and transects of various sizes are mapped directly or by means of photographs. The first employs plane-table and alidade, but its advantage in permitting the insertion of greater detail is often more than offset by the time and labor involved. Photographic mapping is incomparably more rapid and can be made to supplement the quadrat views with the desired adequacy. For maximum detail, an elevated platform is used, preferably on an auto-body for mobility, though a stepladder may serve as well. To permit tracing the changes from season to season or year to year, the exact location of the tripod is fixed, originally by means of three stakes as in a tristat, and later by a single one at the end of a plumb-line, or by a focusing stake and centering dot on the ground-glass. Panoramic cameras may be employed in this work, though a certain allowance must be made for marginal distortion. Panoraming with a Cine-Kodak is much more satisfactory, especially when kodachrome film is used, since both

the large scale and color aid greatly in revealing details. Finally, community maps on a small scale are best made from an airplane, but these naturally must be combined with detail maps and other records made on the ground.

Indicator Methods.—The role of comparative observation in the analysis and correlation of vegetation is a large one when it uses plants as indicators of conditions and processes and hence of land use and recovery. Every species is an index to the physical factors of its habitat, whether climax or seral, to the effect of disturbance, the course of succession, and often also to the influence of animal coactions. As such, its value is greater in terms of the community to which it belongs, and hence the latter constitutes the best type of indicator, since it integrates the response of a considerable number of species as dominants.

The indicators of paramount importance are the dominant species that constitute a climax, since they bear the unmistakable impress of the climate in the corresponding life-form, viz., tree, shrub and grass. The same correlation extends into subforms, such as coniferous, deciduous, and sempervirent trees and shrubs, and sod or bunch forming grasses. As a corollary of the first significance, climax indicators express the type and degree of climatic control and the problems that confront man in his utilization of the region concerned, either in maintaining the climax or in modifying or replacing it permanently. The indicators of the various stages of succession toward the climax are often of equal importance, inasmuch as they reveal the course of development and provide the readiest tool by which the return of the climax may be hastened, retarded, or prevented, or the movement deflected into another path. Of seral indicators the most practicable are the dominants of subseres, since these arise from disturbances. They not merely denote the nature of the disturbing process, but likewise its course and the manner of manipulation necessary to bring about the desired type of permanent community, which is often the subclimax, or more rarely a seral stage.

As examples of the above, there are a number of subclimax trees of greater commercial value than the climax dominants that they have replaced, notably longleaf pine (*Pinus palustris*) and Douglas fir (*Pseudotsuga taxifolia*). Such stands can be maintained against the return of the climax dominants only by means of fire, but when this tool is used too frequently, unintentionally or otherwise, the subclimax is itself displaced by an earlier seral stage. The same general relation prevails on grazing

ranges, in which short grasses have everywhere increased under intensive utilization, but are in turn dispossessed by less valuable seral dominants under serious overgrazing. The mid grasses relict in such disclimaxes not only indicate the original mixed prairie climax, but their condition and abundance also determine the treatment needed to restore them to their proper rank in the regenerated range.

Fields of Application

General Relations.—While ecological methods and concepts have been utilized for some time in agriculture, forestry and grazing, more recently their use has been much extended largely in consequence of the growing appreciation of quantitative values, as well as of the need for cooperation between dynamic ecology and the specialized fields. The latter in particular has led to the recognition of the role played by different types of communities in terms of influences or reactions, with the logical though not altogether desirable result that erosion control projects have been initiated in all three fields. Grazing had already come to play an important part in the administration of national forests and was necessarily concerned in the plan for the so-called desert homesteads. It is likewise the major consideration in the organization of grazing regions and districts on the public domain.

Land classification for optimum use has been conspicuously absent until recently, but critical conditions in the West during drouth periods require some intelligent consideration of its necessity. This is indispensable to the selection of the regions and the actual areas to be protected by the windbreaks of the so-called shelterbelt, and it is equally involved in all projects for erosion control and water conservation. Less dramatic but still of great importance is the protection of modern highways against erosion and the consequent economy of maintenance, and with this must go a proper concern for ornamentation. In addition to highways, control and beautification through landscaping are needed in practically all natural parks, whether national, state or county, and control and restoration are requisites in many other units, such as recreation grounds, game refuges, research and wilderness areas, etc. Finally, climatic factors often play a decisive part in all uses of plant cover and no project is complete without taking definitely into account the wet and dry phases of the 11-year cycle in particular.

It is evident that these fields and related projects are largely a matter of specialization and to a certain extent of tradition in terms of administration. Any one of the major projects may and usually does broaden its scope to include areas that belong in the strict sense to the others and thus any natural limits disappear. While this has been inevitable up to the present, it is regrettable and must be remedied to an increasing degree if the best practical and scientific results are to be obtained. It is quite impossible to deal adequately with one type of vegetation in any region without consideration of the others, while in terms of basic processes involved, all climaxes are closely similar. This is well exemplified in the case of the shelterbelt, in which the task devolves upon the forester by virtue of the use of trees, though the climax and climate concerned are those of grassland. Hence, while the following treatment is organized on the basis of projects, it cannot be too strongly emphasized that this violates every canon of dynamic ecology and that a proper ecological synthesis is imperative if rehabilitation and restoration are to achieve the necessary measure of success.

Land Classification and Use.—The major features of a comprehensive land policy based upon the methods of dynamic ecology were outlined long ago (1910, 1920), and only the essentials are repeated here. The first of these is that land must be classified on the basis of optimum permanent use, and the second that the lands of a general climatic region or district are to be correlated in such a manner as to supplement each other. The third principle is that proper heed must be paid to the climatic cycle in classifying and much greater weight assigned to the unfavorable dry phase, which demands a complete reversal of the existing practice. The fourth essential is that land should improve or at least not deteriorate under utilization, and the last is that it must maintain an assured basic role in the economical-social welfare of the region.

It cannot be too strongly emphasized that no classification worthy of the term was applied during the settlement of the lands of the West in particular. Even the one or two endeavors have been rendered abortive by political pressure, the demand for haste, and the general lack of a trained personnel. However, the classification under the desert homestead act did recognize the unique importance of native vegetation as the basis for evaluating land, and hence marks the first real step in advance. The natural plant communities are not merely the best integrators of the effects of climate and soil, but axiomatically they are also

Successful operations in clearing overgrazed range: King Ranch, Kingsville, Texas.
A. Condition of range before clearing: mesquite and cacti have replaced grasses eaten by cattle and rodents.

by far the best judges of these two complexes in terms of plant production. When reinforced by the composite judgment of all the practical experiments in a region and checked by an understanding of the inevitable climatic cycles, they can be trusted to furnish the basis for the highest type of social-economic development possible in a particular climatic region.

No such convincing proof of the unwisdom of attempting to settle land by the trial-and-error method has ever been afforded as that now available throughout the Great Plains, but disasters comparable in most respects have attended every great drouth period, as in the early seventies, the nineties, and 1917-18. Drouth itself is inevitable at more or less definite intervals (Clements, 1916, 1921), but the major damage is done by man's failure to heed the climatic indicators as to use and to control the destructive processes that he sets up, and his incurable optimism as to the effect of cultivation upon rainfall. Some of the damage wrought by the failure to classify land and direct its use may still be undone by applying the proper principles and methods, not merely to the new appointment of the public domain but even more helpfully to the reclassification of all so-called marginal lands and their rehabilitation on the basis of the climax vegetation. Classifications as to the capacity of the land and range conditions, now in use by the Soil Conservation Service, embody the features set forth in the foregoing.

Grazing and the Public Domain.—The first application of quantitative methods to the problems of grazing came in 1905 with the organization of the national forests and the necessity of finding a basis for grazing allotments, which led to the use of quadrats in connection with reconnaissance and especially on the grazing reserves that were soon established. These were designed primarily to insure regulated utilization together with the gradual improvement of the range, and it was not until 1918 that an ecological system of closures, quadrats and transects was established on the Santa Rita Reserve in southern Arizona, as well as in the northern part of the state, at the Mandan Station in the Great Plains, and elsewhere.

Because of their low stature, relatively short life-span, and quick response to conditions, grasses lend themselves more readily to experimental studies than do the taller and slow-growing trees, though the principles and methods are necessarily the same for both. While the major purpose in the study of grazing ranges is to secure the proper

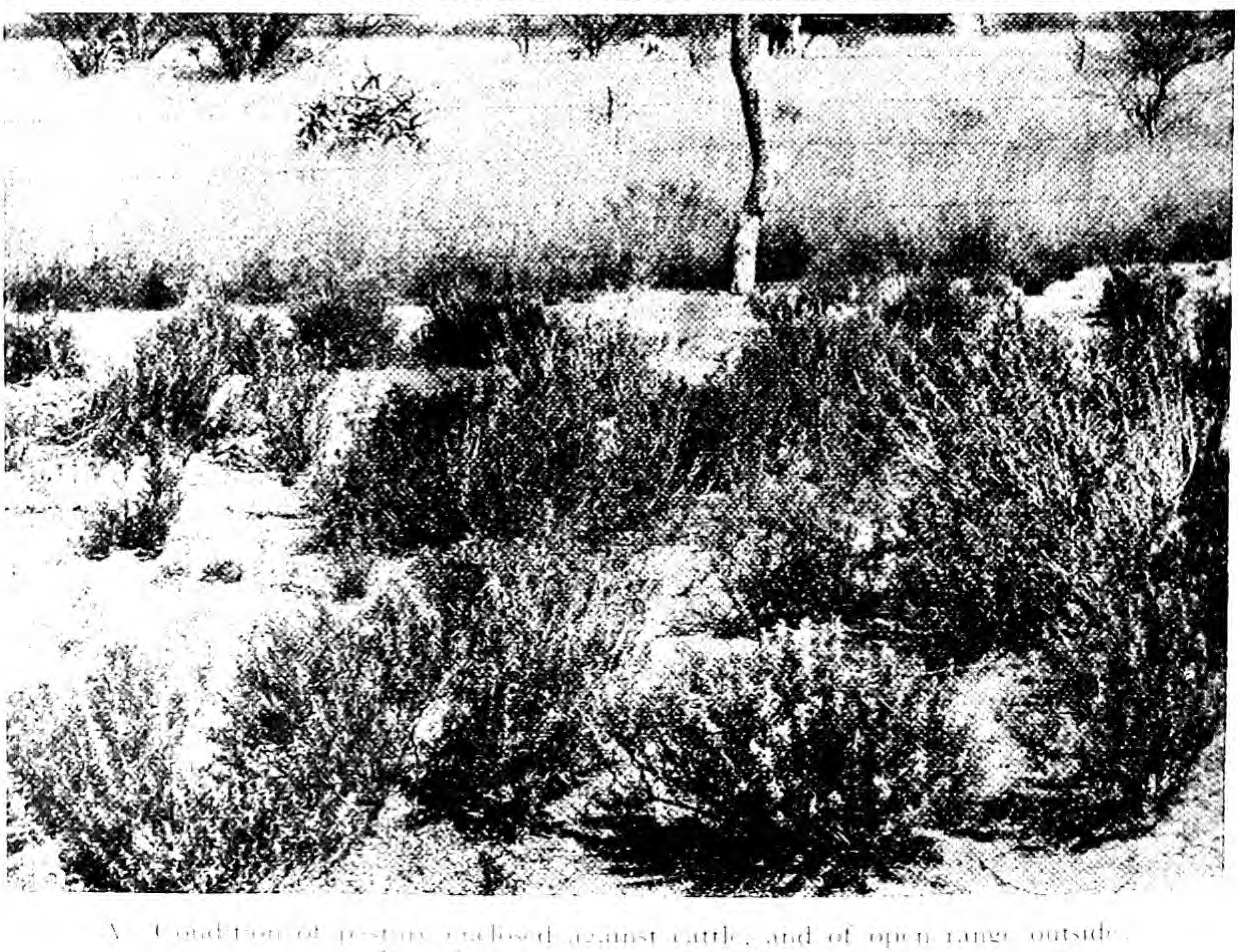
Operations on King Ranch, Kingsville, Texas.

A. Land cleared of mesquite and cacti, leaving occasional mesquite for shelters.

B. Crop of Rhodes grass (*Chloris gayana*) grown on the cleared range.

balance between use and improvement, this can be obtained only through certain immediate objectives. The chief of these are a working knowledge of grazing types in terms of climax and climate and of the effect of succession, an understanding of the seasonal and competitive relations of the dominant grasses and associated forbs, the coactions of cattle with especial reference to overgrazing, the effects of rodents and their predators, the role of drouth, the moot question of direct improvement by sowing and planting, particularly of foreign species, and the reaction of the grass cover itself upon runoff, flooding, erosion, and water supplies. In short, a grassland climax embodies all the responses and effects of a forest, though in different form and degree (Plates 61 and 62).

Even the most succinct account of the progress of research in these respects is impossible here and it must suffice to sketch in the boldest outline the chief methods and results. First of these is the exclosure, which in combination with the enclosure, or pasture in the regular form, permits a relatively accurate measure of the effects of the several processes involved. The simplest exclosure affords protection against cattle alone and makes possible the measurement of the consequent improvement or recovery, its rate, the effect of the grazing practiced, the outcome of competition between the preferred grasses and the less palatable forbs, etc. The part taken by rodents in all this is often very considerable and consequently rodent-proof or total-protection exclosures are added to the installation. Impressed upon all these effects, obscuring or emphasizing them, are those of the year, which in turn vary greatly with the phase of the climatic cycle and require measurement likewise, such as is provided by the isolation transect or cycle exclosure (1920, 1929). However, all of these deal more directly with effects than with causes and for an adequate ecological analysis of the processes involved in overgrazing as well as restoration, it is necessary to isolate each and follow its course under control. This is done by means of a process or conversion series, which may be installed in any exclosure but is most conveniently duplicated on each side of the boundary fence between cattle-proof and rodent-proof units. Such a series may deal with one or more of the processes of major importance in the type concerned, but preferably it should take them all into account for the sake of a complete and objective analysis. The most important of these are grazing, usually simulated by clipping, burning, erosion, denuding, such coactions as trampling and burrowing, competition, seeding and planting (Plate 63).



A. Condition of pasture enclosed against cattle, and of open range outside. Page Ranch, near Tucson, Arizona.

B. Experimental exclosure against both cattle and rodents, Santa Rita Range

The use of ecological methods of measurement and experiment in the past has disclosed a number of principles that appear to be of universal significance, some of which may well be regarded as axioms. Chief of these is the irresistible impulse toward the climax, which can be slowed or halted only by deep-seated disturbance or by unfavorable climatic swing. A major corollary is that the climatic life-form everywhere maintains its ascendancy in the absence of disturbing processes and reasserts it as soon as these are removed. So far in many hundreds of cases no exception has been found to the rule that grass dominants vanquish forbs and annual grasses on the one hand, and bushes or shrubs on the other whenever grazing, fire or similar destructive disturbances are prevented (1920, 1928). The correlation of control with climate is even more exact, operating within the grass life-form to the extent that mid grasses, such as *Stipa*, *Sporobolus* and *Koeleria*, yield to short grasses in semiarid climates and to tall grasses in more humid ones under the impact of grazing, mowing and fire, and reclaim their climatic dominance when these forces are eliminated. Another expression of this principle is found in the fact that the grasses of a particular climax are the best adapted to its climate and have a distinct advantage in terms of competition over introduced ones. This applies with especial force to the world-wide search for grasses to regenerate the open range and to aid in erosion control. The chances are all but decisive against the success of such efforts at introduction, as the actual attempts in the past have demonstrated.

Public Domain.—At present the unreserved public domain consists almost wholly of semiarid or arid grassland and desert, valuable only for grazing and as watershed, or for neither over considerable portions of it. The value of practically all the usable parts has been diminished by overgrazing and erosion, aided by recurrent drouth, and the task of the Bureau of Land Management is to develop systems of range control that will restore and conserve the natural forage crop. For this, a comprehensive system of exclosures has been proposed, designed to evaluate the present grazing capacity of the various grazing types, the rate of recovery to be expected under proper regulation, and the method of securing the best balance between utilization and conservation. A necessary adjunct is the use of indicators to record existing conditions and their gradual change into grazing communities of the desired composition and yield.

Shelterbelts and Windbreaks.—The controversy that still rages over the wisdom of the shelterbelt project may well be regarded as a major argument in favor of making the experiment. The need for relief from want as well as from dust storms requires no argument and the other moot questions are susceptible of objective demonstration in the course of providing the succor demanded by the conditions. It is evident to those with wide ecological experience that the merits of the project are overestimated by those who feel that tree planting is a panacea, just as its difficulties and impossibilities are alone visible to the critics of the experiment. Granted that the form in which the plan was first made public was impossible, the fact remains that trees have been grown with much success within the limits of the belt proposed and that such windbreaks have been of value in a number of the respects claimed. No qualified student of vegetation, in its water-relations especially, expects windbreaks to modify the general climate and particularly in the direction of increased rainfall, but the local influences have already been demonstrated and some of them measured.

The ecologist familiar with the region, recognizes nature still maintains trees in portions of it, notably in valleys, in the higher foothills to the west, and in areas to the east or north where rainfall is greater or evaporation and transpiration less. Planting has had notable success in the sandhills of Nebraska, offset in some measure by corresponding failure in other sandy stretches, and the earlier establishment of windbreaks has a considerable number of successes to its credit in spite of the drawbacks of a cooperative arrangement. Trees can be grown in the zone as now outlined, though forests cannot, and the major questions are those of extent and size. These can be answered only by the actual trial, in which the selection of proper sites and suitable species are the paramount problems. A close second in importance is the preparation of the ground, the form and structure of the belt, protection against animals, and the precautions against the return of the climax grasses. Finally, the unique value of the project as an experiment on a grand scale will be lost if every consideration is not given to obtaining the most comprehensive and objective measures of effects, in so far as these have to do with reactions upon air and soil, the competition between windbreaks and crops, and the coactions of animals.

From the very nature of the grassland climate and climax, it is probable that extensive areas within the belt will be inhospitable to trees

and that with these recourse must be had to the restoration of the original grass cover or an approximation to it. This is even more certainly the future of marginal farm lands to the westward, which is destined to return to grass by default, or better by means of a comprehensive and properly articulated plan for rehabilitation. The entire region between assured agriculture on the east and the mountains has been the center of a cyclic ebb and flow of human populations to the point where illusion as to its possibilities of utilization for cereal crops is no longer possible. However, this tragic process is bound to continue until the clear evidence of climate and climax is heeded, the land classified as grazing country and its organization into proper holdings directed by the federal authority.

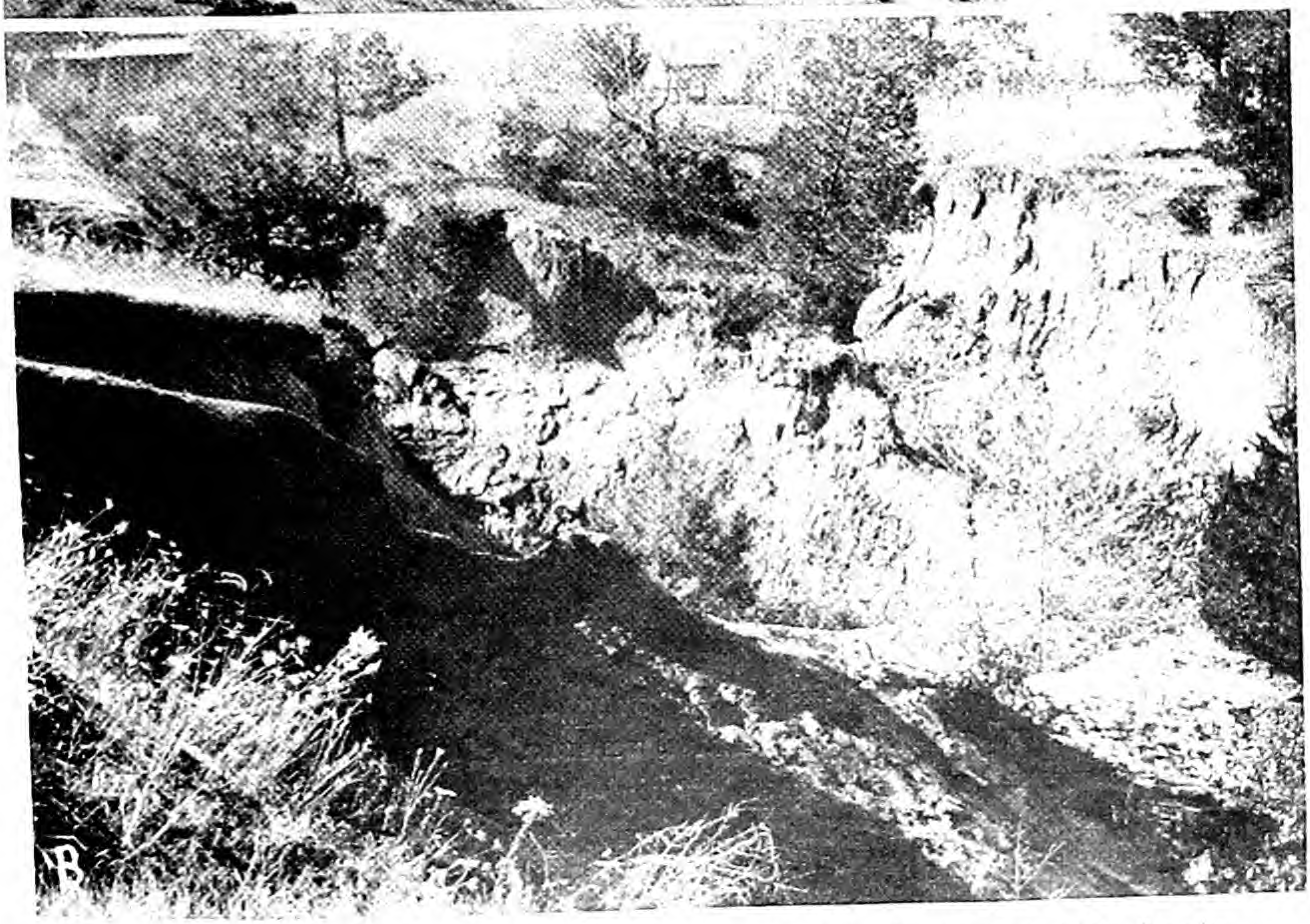
In the three great aspects of the shelterbelt project, ecological considerations necessarily reign supreme. The method of indicator communities is indispensable to the selection of site and species, and it may be epitomized in the statement that climax areas are the most difficult of conversion and control, while seral, subclimax and postclimax sites hold out the greatest promise. The preparation, development and maintenance of the windbreak communities are almost wholly dependent upon the understanding and control of such processes as reaction and coaction, in which man may easily become the adverse element through omission or commission. As to the influence exerted by the windbreak, this is primarily a matter for measurement by means of instrument, phytometer, and quadrat, both within the community itself and its zone of influence, as well as by comparative determinations outside the latter. Since water relations are of the first significance, the phytometer has a peculiar value in determining the water use of the elements of the windbreak, and of the cultivated and native crops under its protection. Accurate knowledge of the transpiration of the various life-forms and species in all three of these will have a decisive bearing upon the question of possible benefits (1924).

Runoff and Erosion.—Every agency that destroys the vegetative cover and exposes the surface of the ground gives opportunity for erosion and flooding in proportion to the completeness with which it acts. However, all such places constitute initial areas for succession, as a consequence of which the soil again becomes increasingly protected by a series of communities.

Such a protective function is peculiarly the property of the subsere,

since this is initiated by disturbance on a soil readily susceptible to wear. In the case of typical priseres, on rock or in water, neither medium is capable of erosion and the seral stages are in full control before soil in the usual sense is available. The process is even more completely one of succession than in the projects already discussed and lends itself all the more readily to ecological procedure. It embraces destructive coaction, either progressive or recurrent, at the beginning, with reaction and competition as the forces that bring about increasingly greater control of the surface and upper layer of the soil until the subclimax or climax is attained. The rate and amount of reaction are functions of sere and climax and though they agree in general terms, they differ in detail for forest, scrub, grassland, desert, and cultivated areas, as they do in lesser degree for the varying types of these communities.

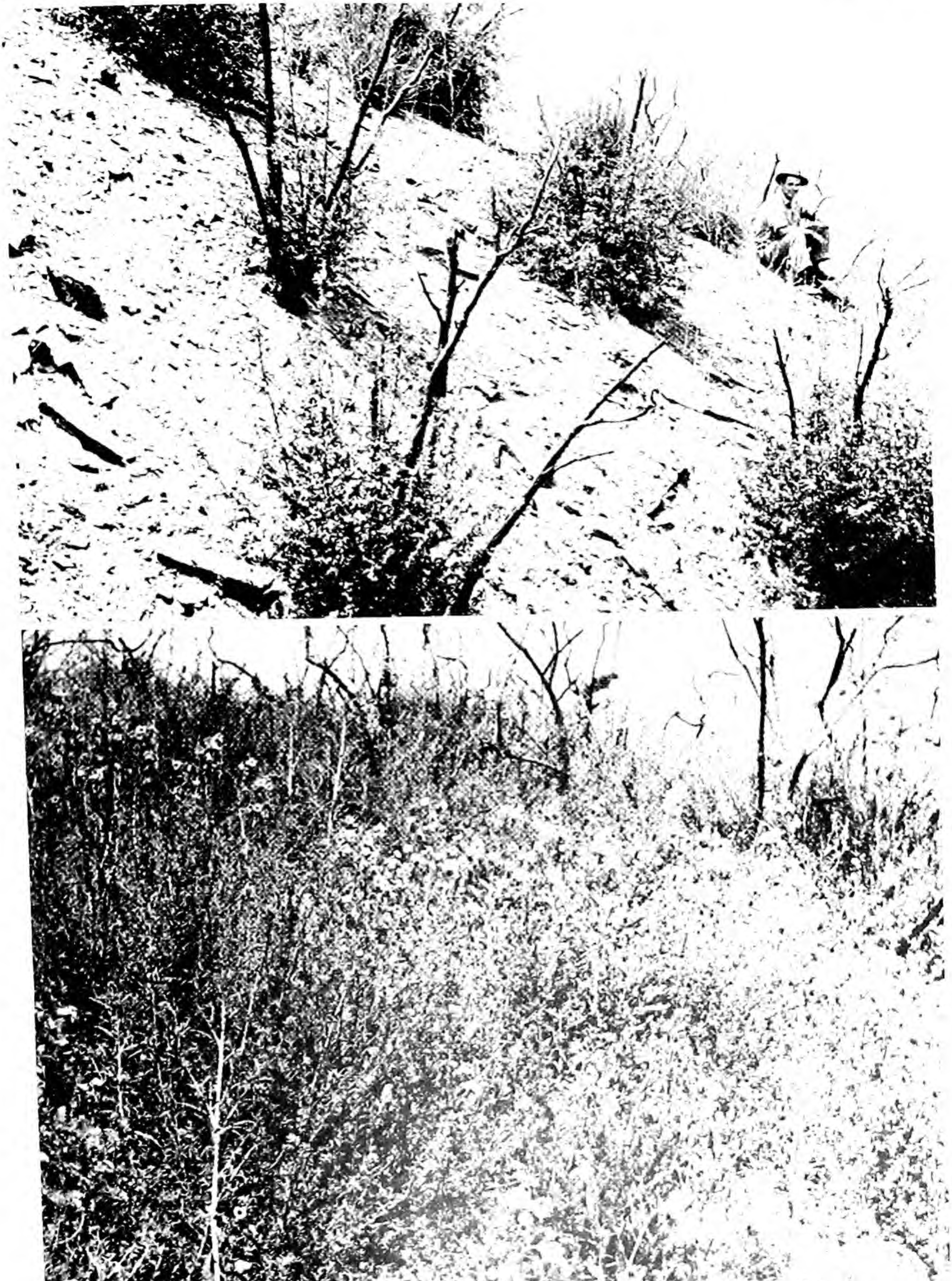
Though erosion is usually the most evident of the processes concerned, it is but one of the interactions between climate, vegetation and soil, in which the plant cover is the decisive feature. The simplest relation is to be seen in erosion by wind, either in dunes where a constant supply of sand is available, or in semiarid regions where the soil remains exposed for considerable periods as a result of cultivation, especially in systems with fallow. When cropping is pushed beyond its proper climatic limits in consequence of a wet phase and economic factors lead to extensive ploughing under and abandonment of fields, the next drouth period of the cycle cannot fail to bring dust storms, shifting dunes of top soil, and attendant disaster (Plate 64A). In contrast, erosion by water is far less dramatic except in times of torrential floods, but is much more universal and continuous; the interaction is more complex and the practical methods of control as well as the results are more varied (Plate 64B). It is imperative to take the whole water cycle into consideration to permit a complete analysis and to direct methods and processes to the major objectives. Thus, while erosion begins only when water acts upon an exposed surface, the intensity, direction, duration, distribution and nature of the rain are all of significance, and back of these lie the kind of precipitation, whether rain, hail or snow, its relation to season, year, cycle, etc. Furthermore it is essential to follow the disposition of the water that falls and hence to measure interception, condensation, transpiration, and infiltration by the cover, runoff, evaporation, storage and percolation with respect to soil, and flowage, spreading, impounding and wastage to the sea, as well as in irrigation and urban use.



A. Farm overwhelmed by soil blown from ploughed fields, Springfield, Colorado
B. Farmland washed away by unchecked water erosion, Waynesboro, Tennessee

While cover is the supreme factor in erosion and flooding, its effectiveness exhibits the widest range by virtue of differences in life-form and composition, height, density, root system, and seasonal duration, as well as in the characteristic litter. In terms of canopy and litter, forest produces the greatest reaction, followed by chaparral and other scrub, while grassland binds the soil with roots as no other community does, though cereal crops naturally approach it in this respect. Broad-leaved forests generally surpass coniferous ones, and deciduous ones are the least effective during the resting season. However, deciduous foliage transpires more than other types as a rule and reduces the water content correspondingly, while the water loss of grasses is determined by their structure and size, the tall grasses approaching that of deciduous margins and exceeding that of evergreen chaparral. These relations are naturally reflected in the subsere characteristic of the different climaxes and especially of the several types of disturbance. Fire has a profound effect upon woody communities and the regeneration of the cover is a slow process, except in such root-sprouting types as the chaparral of California. If not too frequent, it affects grassland little, but the reaction value of grass may be seriously reduced or almost destroyed by overgrazing. In accordance with its completeness, clearing is destructive to all protective reactions, especially in the annual harvesting of many crops, and construction is often but a specialized type.

All the disturbances that affect the protective role of covers are universal in settled regions, but they are most portentous in those with relatively low rainfall, where conservation is the critical need and where recovery of the vegetation, by natural or artificial means, is less rapid and thorough. Floods are more frequent and extensive in humid basins, but their control through vegetation is naturally a much simpler affair. In the climate and topography of southern California, the number of undesirable events that flow from the burning of chaparral is probably to be equalled nowhere else, when population and productivity are brought into the picture (Plate 65A). Quite apart from the destruction of beauty and of recreation sites, the modified water cycle carries with it material damages of the most serious character. This begins with increased runoff and the accelerated removal of litter and humus, passes into rilling and gullying, flooding and flows of mud and debris, with accompanying disaster to human communities, and ends in the sealing of gravel basins, the silting up of reservoirs, pollution of urban supplies,



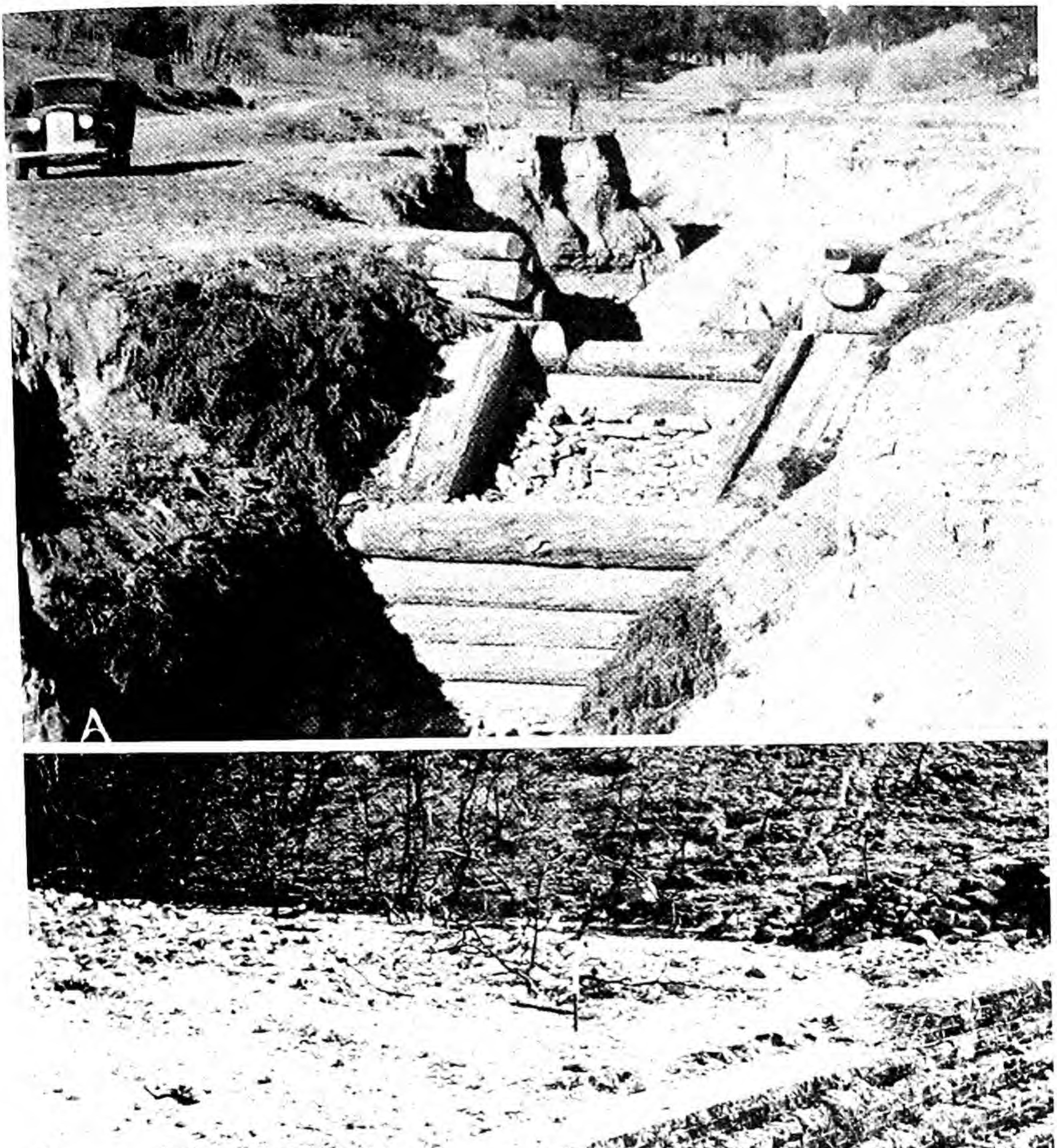
A. Mountain slope denuded of [illegible] Santa [illegible] Mountains [illegible]
B. Natural succession [illegible]

and enormous losses of priceless water to the ocean. The re-covering of the denuded slopes by natural succession gradually becomes more and more difficult, transpiration and evaporation are progressively lessened, and the local climate changes for the worse.

In the case of chaparral, as with other root-sprouting dominants and with the rapidly growing fire pines or jack pines, natural recovery regularly ensues in an adequate degree where burning is not too frequent. The succession in chaparral regularly begins the first winter with an astonishing growth of annual forbs, which usually yield the second or third season to perennials, especially grasses at lower elevations, and these in turn are displaced by the competition of the root-sprouts and seedlings of the shrub dominants after four or five years. However, along the ranch front, fire may occur too frequently or dry seasons may intervene to retard succession; the terrain may be too steep and rugged for a protective stand, or the buried seeds of forbs or the root-crowns of shrub and bush may be killed by intense fire (Plate 65B).

Even more serious is the fact that rain starts in the fall before the annual cover can appear and downpours often occur before this has attained sufficient density to be more or less effective which is the situation that caused the tragedy at Montrose in 1934 (Plate 5). In all these cases, nature must be aided and the initial stages of succession hastened and their area extended by sowing. In California, red and black mustard are perhaps unsurpassed in this role and extensive districts have been sown in the Santa Ynez and San Gabriel mountains to retard the silting up of urban reservoirs and to prevent the repetition of disastrous floods. In this, opportunity has been afforded for comparing sowing by CCC crews and by airplane in terms of effectiveness and cost, and the quadrat method is also being used for comparison of natural and artificial succession, as well as the final outcome of the competition between the natives and mustard. The results hold much promise for all situations in which rapid recovery is the critical necessity (Plate 7).

Back of all these immediate problems lies the much debated question of the role of cover in general and forest in particular as a source of material for rain or an agency for increasing the local effect. It must be fully recognized that there is no adequate proof that the planting of forests augments rainfall, though some of the supposed instances cannot be summarily brushed aside. However, it cannot be gainsaid that

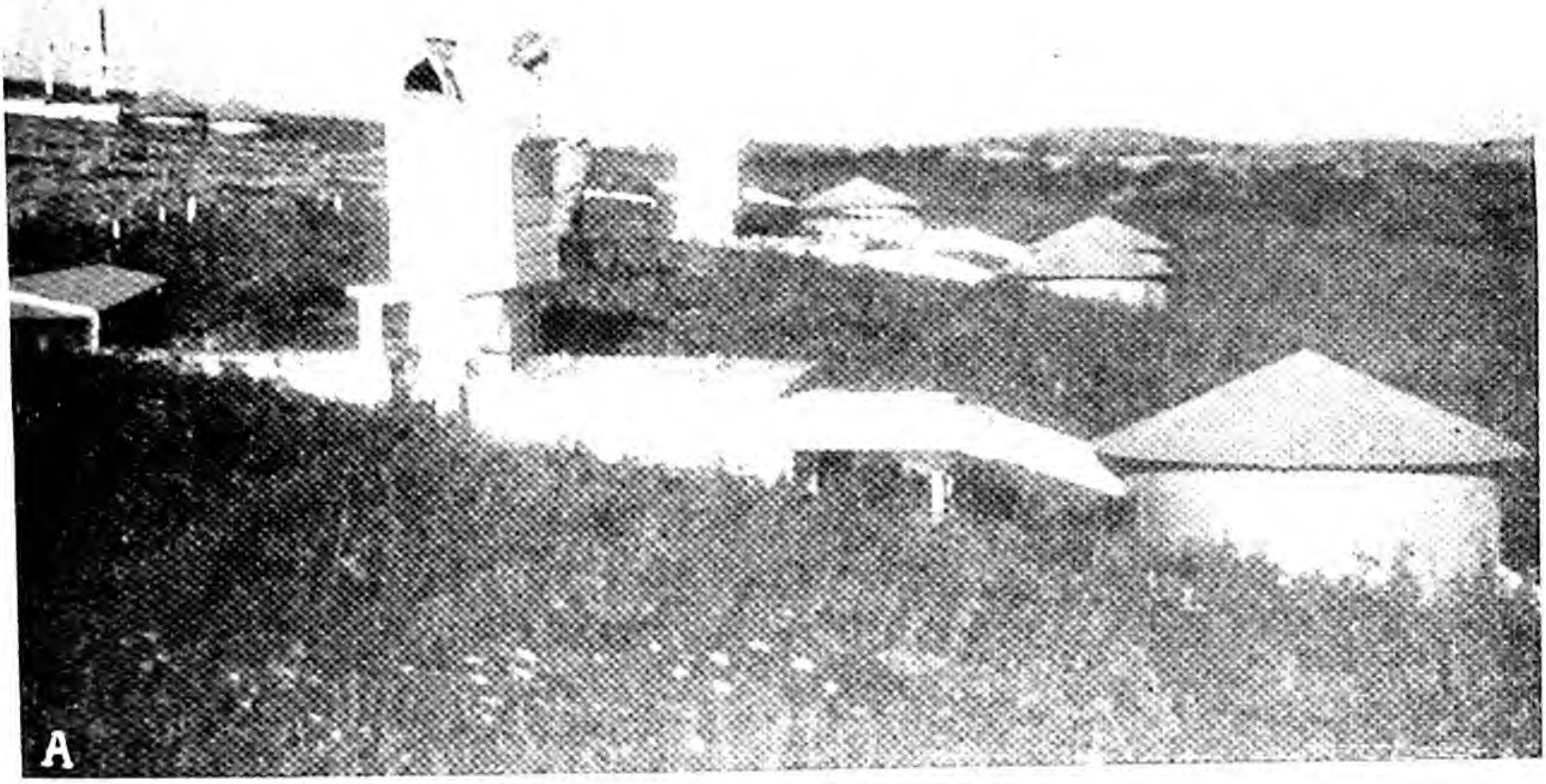


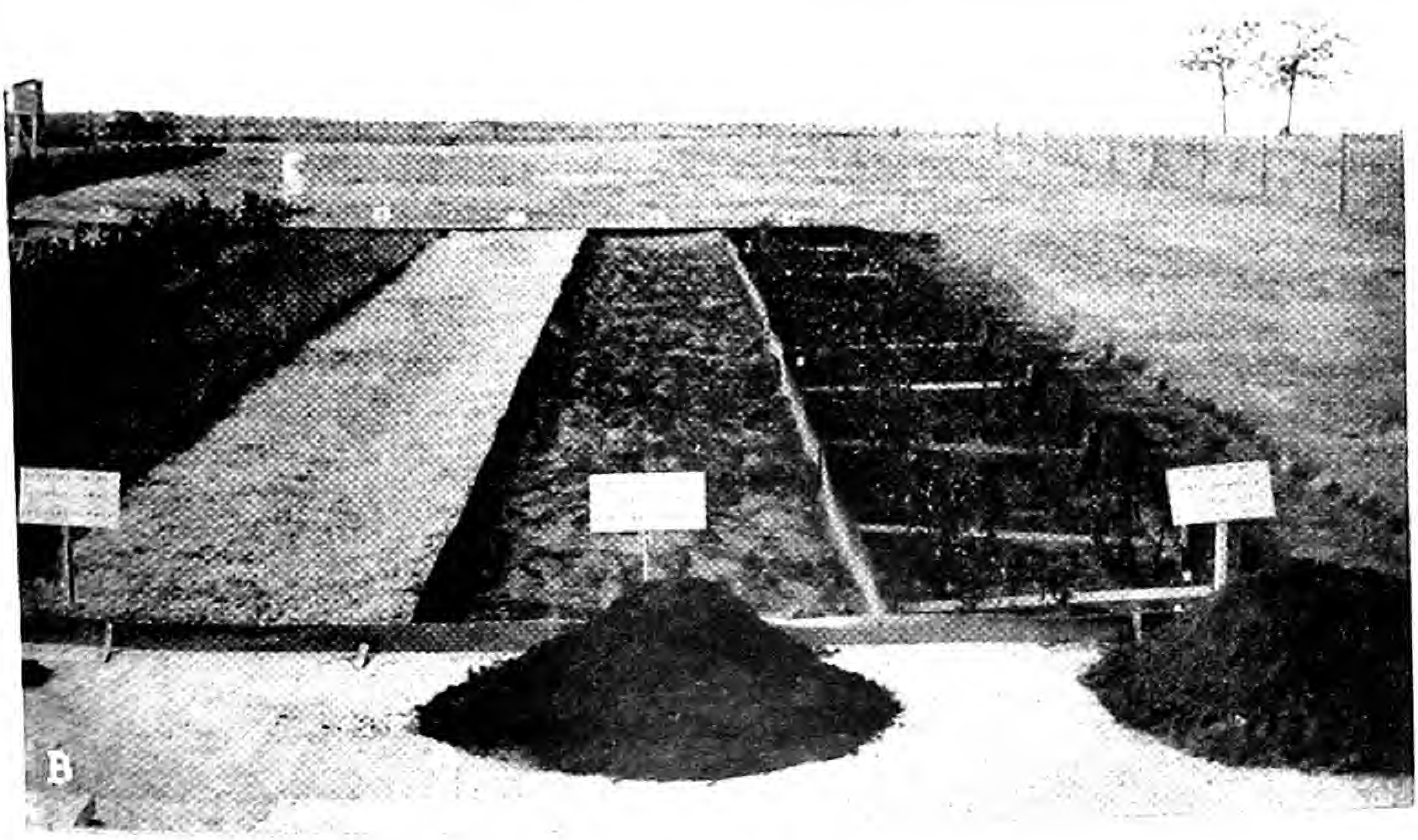
A. Check-dams on the Navajo Indian Reservation, Mexican Springs, New Mexico.
B. Debris basin in Haines Canyon above La Crescenta, California.

deciduous forest in summer may transpire more water per unit area than a body of salt or fresh water, and hence the hardwoods of the Southeast in their virgin condition constituted in rainfall effect an extension of the ocean to several hundred miles inland. This contribution has been decreased by cropping, but the crops of the prairie region transpire in much the same order as the original grasses, a fact that argues strongly against any material increase in the rainfall of the Middle West during the period of settlement (1924). The role of vegetation in providing moisture for local rains is perhaps nowhere more clearly suggested than on Pikes Peak, where convection thunder storms occur at the same general time each day for much of the summer, after transpiration has reached a certain level determined by the seasonal growth. Conversely, the amount of water transpired represents the toll taken by each type of community for the protection it affords, and this is a matter of prime importance in evaluating the reaction of the various life-forms, tree, shrub, grass, and forb and in different sites, such as climax slope and postclimax canyon floor. For all these reasons, the use of phytometers of the various life-forms concerned is an indispensable feature of the major installations for investigating the water cycle, and these are combined with lysimeters to determine the partition of the water that enters the soil.

While cover and succession must be used as the major tools in the control of erosion and flooding, it is obvious that engineering works are indispensable complements in many instances, though it is unfortunate that trust has too often been placed in them alone. The more progressive engineers are coming to realize that the proper place to control runoff and erosion is at the start and that check-dams and debris basins are temporary or supplementary devices chiefly needed during the period when the conquest of fire and the restoration of the natural cover are barely under way. Many small check-dams at the heads of small rillways or gullies are far preferable to much larger ones in ravine or barranca, and valuable as debris basins may be in halting or diminishing the momentum of flood materials, it cannot be denied that the adequate protection of the native cover will render them unnecessary (Plate 66).

Three general types of measures are used to determine the amount of runoff and erosion in relation to the several kinds of disturbance and the stages of the natural or artificial succession that ensues. The simplest and most extensive is stream gauging, which possesses the advantage of





Runoff Erosion Plots

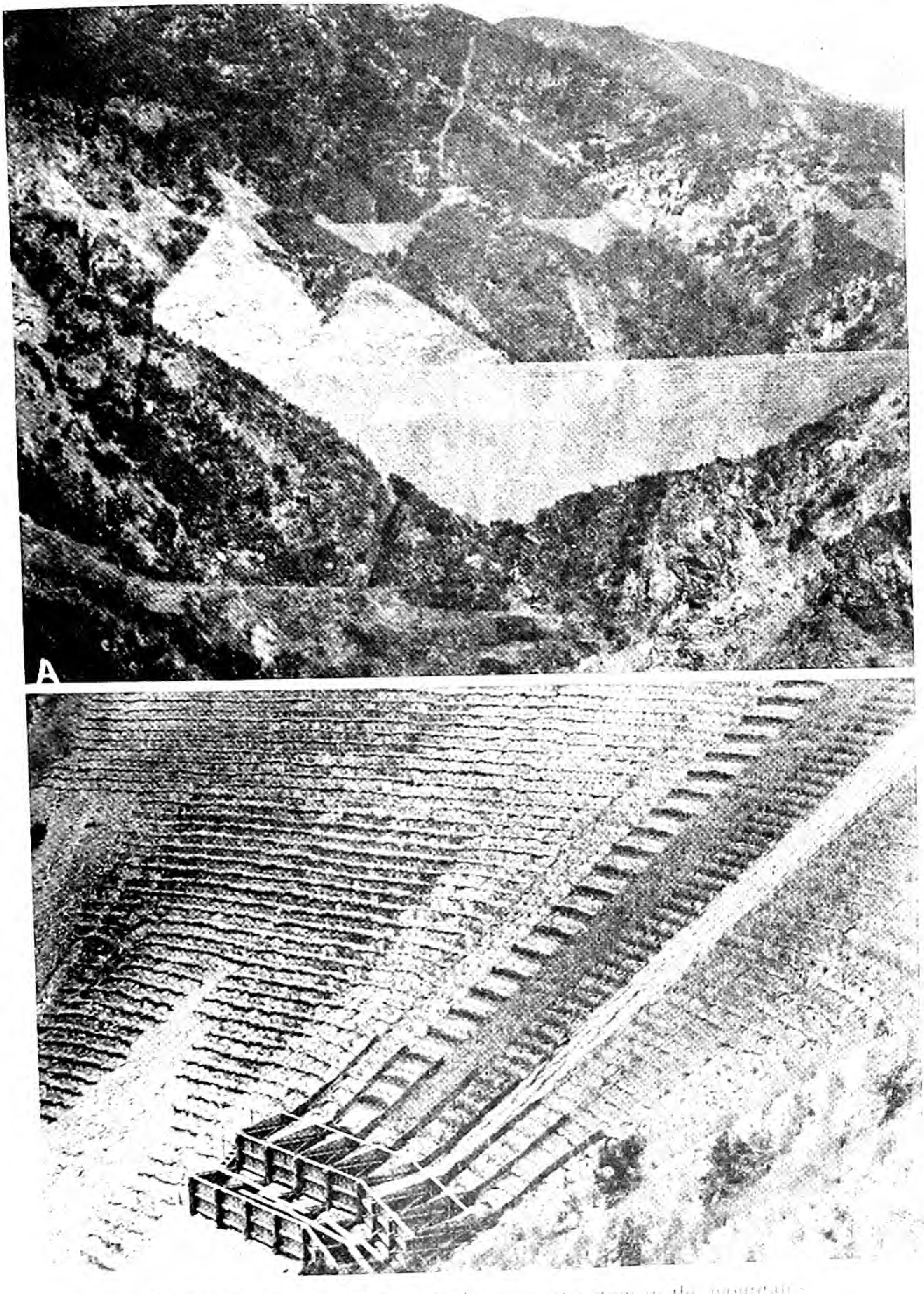
A. General view of installation, showing plots and instruments for measuring eroded soil, Beemerville, New Jersey.

B. Comparative loss of soil per acre on plots at Guthrie, Oklahoma: (1) Bermuda grass: .02 ton; (2) Hard fallow land: [illegible] tons; (3) Plot planted to cotton after 10 inches of top soil was removed: [illegible] tons. Soil Conservation Service.

integrating watersheds of considerable extent, but this is largely offset by the number of variables both in terrain and cover. Watersheds up to at least several hundred acres in size permit closer and more detailed correlation by means of measuring weirs and flumes, especially when topography and vegetation are sufficiently similar to allow installation in triplicate. However, the most intensive measurement can be obtained only from runoff-erosion plots, in which the interaction of cover, water and soil can be traced in minute detail. Such plots are essentially transects placed lengthwise of the slope, 2-4 times as long as wide and of such dimensions as to give an area of 100 square meters, or an aliquot or multiple of it. They are enclosed by a low board wall with an outlet at the bottom into a recording gauge. The plots are arranged in pairs or paired series with a control of the existing cover and such disturbances as are germane to the type, viz., burning, grazing, trampling, denuding, sowing, planting, etc. The course of succession is traced in detail by means of quadrats where these are feasible, or better by a series of overhead views covering all or most of the plot (Plate 67).

Natural Landscaping.—The rapid growth of interest in this field has sprung largely from the construction of modern highways in such manner as to accommodate grades and curves to higher speeds, thus requiring more, longer, and deeper cuts and fills. Engineers were apparently entirely unprepared for the effects produced by heavy rains upon the little consolidated fill slopes in particular, and it required a season of above-normal rainfall to supply the needed arguments of harmful mud flows and excessive costs of repair and maintenance to bring recognition of the problem. Here again, there was immediate need for a protective cover on loose soil, devoid of germules, and recourse had to be taken to planting and sowing. At the same time, the soil was to be held against the combined action of slipping, slumping and washing, and an initial reaction produced by a terrace supported with stakes and reinforced by wattles. This was supplemented by cuttings to carry the binding effect deeper by means of roots and to break the impact of rain by means of crowns, in which procedure *Salix* proved less satisfactory than *Baccharis*, and the reactions were completed by sowing the shelf to one of the grains (Plate 68).

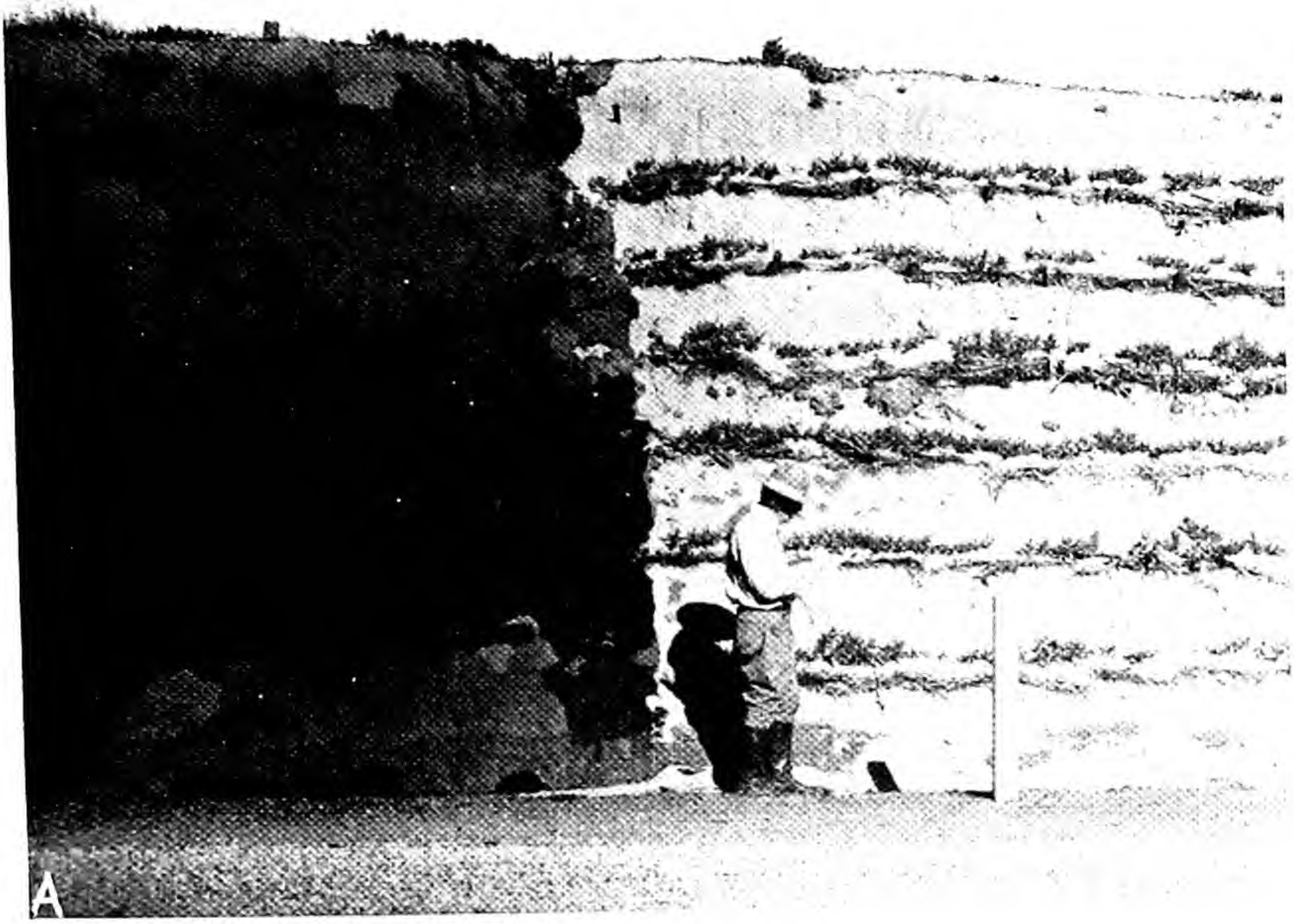
Probably the first organization of guiding principles in natural landscaping and their application on an ecological basis was made in the development of the Blakesley Botanic Garden at Santa Barbara, in



A. Fill slopes resulting from highway construction in the mountains,
San Dimas Canyon, California.
B. Approved method of planting such slopes to prevent soil erosion and slumping.

which several climaxes of the region were combined into a consistent treatment in harmony with the varied topography. The same idea has been used in a smaller garden with uniform terrain about the museum in Yosemite Park, and has also been adopted by two California state parks of very different type, namely, Point Lobos near Carmel and Purissima Mission near Santa Barbara. It has also great possibilities in such restorations as are proposed for the floor of Yosemite Valley, where the original flowery meadows have been entirely dispossessed by weedy grasses, as it does likewise for refuges and reserves of various kinds. However, its outstanding opportunity lies in the treatment of the Wawona Road between the Valley and the Mariposa Grove. To reduce the steep grades, this has been carved out of the mountain sides in such a way as to produce a continuing series of cuts for thirty miles, bald and insistent near at hand and forming an unsightly scar from a distance. These have been organized by sites and units in accordance with terrain and soil, and a detailed plan for preparation and planting worked out for each. One example of each kind has received the necessary reduction or rounding of slope, with protective trenching above and terracing on the face, and has been sown and planted to yield natural patterns in general harmony with the vegetation present. The course and outcome of the succession are being followed by tristat and quadrat, and controlled to insure obtaining the effects sought, and these are to serve as a guide for the ultimate landscaping of the entire highway. In addition, the plan contemplates the enhancement of the original stretches of forest and the many recesses and dells, where soil and water permit installing final compositions without the preliminary successional modification of raw slopes.

Along similar lines, demonstration plantings have been initiated upon several main highways in southern California, where by contrast with mountain roads generally, ornamentation takes precedence over protection, though without neglecting the latter. In addition to cuts and fills, it is necessary not only to take the entire right of way into account, but also to provide fire protection for the adjoining fields instead of the unsightly burning or oiling of the roadside (Plate 69). The details cannot be dealt with here, but the complete plan, based on ecological principles and methods, calls for a unified treatment in which ornamental values predominate, but with adequate attention to erosion control, fire hazard, flow of traffic, and reduced costs of main-



A. Highway-cut oiled and planted with ice-plant on terraces as experiment in methods of erosion control, near Santa Maria, California.

B. Slope on same highway showing advanced stage of protection by ice-plant (*Mesembryanthemum*).

tenance. However, the ecologist concerned with the applications of his work may be interested to consider the more important canons laid down. The chief of these is that nature is to be followed as closely as possible and hence native materials alone are to be used, preferably from the outset but invariably in the final composition. While a natural treatment presupposes the use of species and communities in the regional association or faciation, it also permits modification and enhancement consistent within its limits. The process of succession by which nature reclothes bare areas is to be utilized as the chief tool in landscaping, but the process is often to be hastened or telescoped to secure more rapid and varied results (Plate 70).

Climate and Cycles.—To one not accustomed to regarding ecology as a synthesis, it may seem strange that the ecologist should concern himself directly with climate as such, even though the dependence of plants and animals upon physical factors is fully recognized. However, climate and climax are really twin concepts, and the limits of the one can be expressed with fair definiteness only in terms of the other. Climate is in control of the climax and through this of the soil, and it either initiates or circumscribes the varied reactions by which plants mold or control their habitat and in turn influence climate. In consequence, the ecologist is vitally interested not merely in climatic effects, but also in the processes by which these are brought about and in the causes that underlie the latter. His very devotion to changes and cycles in climax and species must be extended to change in the causes concerned and not without the hope that understanding may lead in some measure to anticipation and even the beginning of control.

If further justification for his attitude be needed, it is furnished by the drouth of 1934-1935 in the Middle West, in connection with which the question has arisen, even among scientific men as to whether the climate has not changed permanently and the country will become a desert. While the answer is a definite and unqualified negative, it is essential to know the grounds upon which this is based. It is equally important though less pleasant to recognize that settlement and cultivation have not increased rainfall, that the winters are not colder and the summers no hotter, and that snowdrifts were not deeper, except relatively, in one's boyhood; in short, that the records prove neither drouth nor abundant rain ever comes to stay, but each comes and goes in a more or less definite cycle.

A. Native lupin ornamenting a roadside in Southern California
B. Tamarisks planted along highway for ornamentation and shade near Yuma, California

It is at least interesting that renewed activity in the study of climatic cycles should have been focused upon the annual rings of trees as integrators and have developed in close touch with researches on climax and succession. From this came further evidence of a probable correlation with the sunspot cycle, its multiples and aliquots, as likewise with the solar constant. There is now general agreement with Köppen's discovery in 1873, that mean temperatures throughout the world are somewhat higher at sunspot minima than at maxima, especially in the tropics. The relation with rainfall is less definite, as well as apparently divergent for certain regions, and agreement upon it is correspondingly less general. In spite of this, an increasing number of investigators in various parts of the world have found more or less correlation, and the chief task at present is to bring the results into general harmony. Because of the critical effect of drouth upon both cultural and natural vegetation, the first ecological investigations in the field dealt with the coincidence of drouth and sunspot maxima. In these it was shown that a drouth period of several years had occurred in the western United States at each maximum of 80 spots or more, and notably in the early seventies and nineties, accompanied by widespread economic consequences (1928).

It was logical that this and related hypotheses should be tested by attempts to make long-range forecasts of rainfall some months or even a few years in advance, utilizing chiefly sunspot numbers which themselves permit prediction in general terms, but employing also the solar constant, ocean temperatures, ice indices for the oceans and other criteria. Some of these have achieved considerable if not noteworthy success, while the ecological efforts in this field led to the anticipation of the drouth of 1917-18 and of the relatively low maximum of 1928 and its indication of no extensive or serious drouth. Later results have justified the working hypothesis that sunspot minima are also times of drouth, an assumption supported by the prevailingly higher temperatures at such periods and strikingly exemplified by the occurrence of unprecedented drouth in the Middle West in 1934-1935. It is unnecessary to point out the significance of long-range prediction for the various projects previously discussed, as well as for the whole social-economic system. Moreover, in spite of the great complexity of the problem, it is fairly certain that marked progress will continue to be made towards its solution.

GLOSSARY

Adaptation—A change in habit or structure in response to environment.

Adjustment—The functional response to stimuli.

Adsere—That portion of a sere that precedes its convergence into another at any time before the climax stage.

Afforestation—The establishment of a forest, either by planting seed or by transplanting trees.

Aggregation—The establishment of invaders into groups of individuals as a result of propagation.

Alternation—The arrangement of the vegetation when conditions change abruptly, such as the occurrence of trees or shrubs on a moist slope or a ravine, but not on the drier areas, or where one type of forest occurs on warm, dry south slopes, and another type on the cool, moist north slopes.

Alternes—The different groupings of vegetation in alternation.

Annuation—Difference in composition and appearance of the climax at extremes of wet and dry cycles; fluctuation of numbers of animals in response to climatic cycles.

Arenaceous
Arenarious } Having to do with sandy places.
Arenicolus

Aspect—The seasonal changes in a community, e.g., the spring aspect.

Aspection—Periodic changes in the appearance of the constituent species, associated with periods of foliation and defoliation, or with periods of flowering, which are reflected in the physiognomy of the community as a whole or of its constituent parts. The periods of aspection are termed seasons or aspects and are of society rank. Those usually recognized are prevernal, vernal, aestival, serotinal, autumnal, and hiemal or hibernal.

Association—All of the life of a given climax area of uniform taxonomic composition. A climax unit with two or more dominants. Climax communities which are associated regionally to constitute a formation. The associations agree with their formation in physiognomy and

development, but differ in floristic composition among themselves, and to some degree in habitat.

Associes—The developmental equivalent of the association; a temporary stage of development; a nonpermanent community to be replaced by another in the process of development or succession.

Associule—A micro-community of associes rank in a serule.

Bajada—The lower slope of a desert mountain, formed by soil washed down by precipitation.

Barrier—A physical or biological obstacle to migration or ecesis; first used by DeCandolle in 1820. Any topographic feature or any physical or biological agency that restricts or prevents invasion.

Biome—A community of plants and animals, usually of the rank of a formation: a biotic community.

Bisect—A cross section of soil showing plant roots and shoots in their normal position.

Boreal—Northern.

Chresard—The available water of the soil; the physiological water content.

Clan—A group of plants composed of secondary species in local or restricted small, scattered areas; a more or less permanent feature of climax communities or of consocies which exist for a long time; a small community of subordinate importance but of distinctive character, frequently the result of vegetative propagation.

Climax—The final stage of a succession which continues to occupy an area as long as the climate remains unchanged. The succession leading to a climax represents adjustment to changing conditions, and the climax itself the ultimate adjustment to a condition of relative stability.

Climax Units—Association, consociation, society, clan.

Clisere—The series of climax formations or zones which follow each other in a particular climatic region in consequence of a distinct change of climate.

Closed Community—A community occupying an area so completely that no additions can be made to it, either by invasion or by the growth of seedlings. A plant community cannot be regarded as completely closed until all the levels for abstracting water, minerals, light

and air are filled with sets of species of dissimilar habits and requirements.

Closure—An area with definite boundaries; as inclosure, exclosure.

Coaction—The interaction of organisms; the reciprocal effects of plants and animals.

Codominant—One of two or more dominants.

Colonist—A species which follows the pioneers and replaces them, forming characteristic and relatively constant communities.

Colony—A group of two or more species that develops in a barren area, or in a community as an immediate consequence of invasion; initial developmental community composed of two or more species, each of which forms a colony. If one species only were present, the individuals would constitute a family.

Consociation—A climax community with a single dominant; a unit of the association characterized by a single dominant; a community of associational rank typically constituted by a single dominant, but also including those cases where organisms normally dominant are present in sparse distribution and have little control over the community.

Consocies—A seral community with but a single dominant; a developmental consociation; that subdivision of a formation controlled by a facies.

Consociule—A micro-community of consocial rank.

Consument—General term for an animal, from protozoans to mammals, from the viewpoint of consuming rather than producing food.

Cosere—A series of unit successions in the same spot.

Disclimax—A modification or replacement of the true climax, either as a whole or in part, chiefly as a consequence of disturbance by man or domesticated animals.

Diurnation—The phenomenon of daily fluctuation in community composition, i.e., within a single 24-hour day.

Dominant—An organism which controls the habitat; an organism so well adjusted to a given set of conditions that it becomes controlling wherever these conditions occur; the chief constituent of a plant community; genera which have persisted through geologic times to the present.

Dominule—The dominant of a micro-habitat; such as a log, carcass, etc.

Ecad—A habitat form due to adaptation; a form arising by adaptation to environment.

Ece—The habitat.

Ecesis—The germination and establishment of invaders; the phenomenon exhibited by an invading disseminule from the time it enters a new community until it becomes thoroughly established.

Echard—The non-available water of the soil from the standpoint of the plant.

Ecial—Pertaining to the habitat.

Ecocline—The equivalent of a micro-climate; a difference sometimes found between north and south slopes.

Ecology—The science of the relationship of organisms to the environment.

Ecotone—The line along which two types of vegetation compete for the same ground.

Edaphic—Influenced or produced by the soil or its contents.

Edominant—Secondary or accessory species that exhibit no dominance.

Edominule—An edominant of a micro-community.

Emergent evolution—Creation of emergence of the new in the evolution of the universe.

Enclave—Open prairie within a forest.

Enclosure—An experimental area which confines animals within its boundaries.

Endemic—Peculiar to and characteristic of a locality or region.

Eoclimax—(1) The climax of a given period of dominance of a specified plant group, e.g., Angiosperms. (See eosere); (2) The climax of the eocene geological period.

Eosere—The development of vegetation during an eon or era; major developmental series within the climatic climax of the geological era.

Estival—Pertaining to early summer.

Estivation—The passing of the summer in a dormant state.

Eudominant—A dominant more or less peculiar to the association of a climax, such as beech or chestnut in their respective communities, and *Sporobolus asper* in the true and *Stipa comata* in the mixed prairie.

Eufluent—An influent more or less peculiar to or typical of an association.

Exclosure—An experimental area which excludes one or more species of animals by fencing or other means.

Faciation—A concrete subdivision of the association, the entire area of the latter being made up of the various faciations, except for seral stages or fragments of the several consociations. Each faciation corresponds to a particular regional climate of real but smaller differences in rainfall/evaporation and temperature.

Facies—(1) A developmental community in the sense of a faciation; (2) The general aspect of a community; (3) A difference in quantity or distribution of a species, especially in the dominance of certain companion species; (4) A dominant species of a community: a distinct area controlled by it, is a consocies.

Family—A group of individuals belonging to one species. It often springs from a single parent plant, but this is not necessarily the case. It may consist of a few individuals or may extend over a large area. Families, however, are usually small, since they are more readily invaded when large, and consequently pass into colonies. (See colony.)

Fauna hygropetrica—Life in inland waters. Fauna which find lodging in that film of water which surrounds the surfaces of stones not truly submerged, clinging to them by surface tension.

Forb—An herbaceous plant which is not a grass; a weed in the stockman's sense.

Formation—The climax community of a natural area in which the essential climatic relations are similar or identical; that unit of vegetation which is the product of, under the control of, and delimited by, climate.

Formation, Closed—A community in which the plants are so crowded that invasion is difficult. (See closed community.)

Geosere—The total plant succession of the geological past.

Gradation—All of the processes concerned in the moulding of the surface of the earth by the transportation of material.

Halosere—A sere originating in salt water or on saline soil.

Herb—A plant in which the stem does not become woody and persistent, but dies annually or after flowering, down to the ground at least; includes both grasses and forbs, and is distinguished from shrub or tree.

Hibernation—The passing of the winter in a dormant state.

Hiemal—Belonging to winter; occurring in winter.

Holard—The total water-content of the soil.

Holism—The principle which works up the raw material or unorganized energy units of the world, utilizes, assimilates and organizes them; endows them with specific structure, character and individuality, and finally with personality, and creates beauty, truth and value from them. The concept of holism, and the whole, is as nearly as possible a replica of nature's observed process.

Hydrosere—A sere beginning in water or moist places.

Influent—An animal member of the biome by virtue of the influence or coaction it exerts in the community, especially with respect to food, material and shelter.

Insolation—Exposure to the influence of solar heat and light.

Intercalation—The insertion of anything between other things; in geology, the intrusion of layers or beds between the regular rocks of a series.

Isohyet—A line connecting areas of the same rainfall.

Invasion—The movement of plants from one area to another, and their colonization in the latter; it is analyzed into migration (the actual movement), ecesis (establishment), and competition.

Lamiation—A layer society in the climax, which is best developed in forests with a canopy of medium density, so that under the most favorable conditions as many as five or six may be recognized above the soil.

Lamies—A layer socies of an associes.

Lociation—A local variant of an association, varying in composition of the important subdominants and influents, as distinguished from faciation, the local variant based on the presence of dominants.

Locies—The developmental equivalent of lociation.

Macchia—Evergreen shrubs of the Mediterranean region, and California chaparral.

Matrix (matrices)—Foundation material, such as the rock upon which lichens grow.

Mesic—Characterized by, or pertaining to conditions of medium water-supply.

Mesocline—A moist, cool slope.

Mictium (mictia)—A mixed community that intervenes between two seral stages or associes; a mixture of species in an area, as contrasted with zoned areas.

Migrant—A plant that is moving from one place to another, or is invading an area apart from its original one.

Migration—Any general movement by which the range of a species is changed. It begins when a germule (or disseminule) leaves the parent area and ends when it reaches its final resting place; it may consist of a single movement or a number of movements.

Migrule—The unit or agent of migration.

Mott—A group of trees.

Ontogenetic—Of, pertaining to, or relating to, ontogeny.

Ontogeny—The life-history of an organism from a zygote or propagule to maturity.

Paleosere—The eosere of the paleozoic period.

Panclimax—Two or more related climaxes or formations of similar general climatic features, similar life-form, and common genera of dominants; relationship is regarded as due to a common origin from an ancestral climax (eoclimax) of Tertiary or earlier time.

Panformation—Same as panclimax.

Perdominant—A dominant species which is present in all, or nearly all, of the associations of a formation.

Perfluent—An animal member of the biome that occurs more or less throughout the formation.

Petran—Pertaining to the Rocky Mountains (U.S.).

Phylogeny—The ancestral history of animals and plants.

Phytometer—A plant measure designed to express the physical factors of the habitat in terms of physiological activities. It consists of plants grown, at least for a time, in the several habitats that are to be compared. Several plants are used in each habitat so that variability of the individual is checked out.

Plant Association—Any group or community of plants taken in its entirety, which occupies a common habitat. (See community, association.)

Postclimax—The formations of a continent stand in a definite climatic relation to each other. A shift in the direction of greater rainfall will permit the more mesophytic to replace the less mesophytic throughout the series, while a swing toward less rainfall will favor the more xerophytic community at each line of contact. The former is termed a postclimax and the latter a preclimax. Major examples of postclimaxes are provided by valleys and canyons, long and steep slope exposures and extreme soil types, such as sand, etc.

Postclisere—The series of formations that arises when there is a major climatic shift in the direction of greater rainfall. (See clisere and postclimax.)

Potential Climax—The climax which will replace that of an adjacent area in the event of a change of climate, i.e., postclimax and preclimax.

Preclimax—A climax of lower life-form than one adjacent to it and resulting from a drier climate. (See postclimax.)

Preclisere—The series of formations that arises when there is a major climatic shift in the direction of less rainfall. (See postclisere.)

Prevernal—Pertaining to early spring.

Primary Succession—Succession arising on newly formed soils or upon surfaces exposed for the first time, which have in consequence never before borne vegetation.

Prisere—A sere beginning with pioneers on a primary bare area; the natural regional succession upon sites undisturbed by man's agency, whether direct or indirect.

Proclimax—A more or less permanent community resembling the climax in one or more respects, but gradually replaceable by the latter when the control of climate is not inhibited by disturbance. Includes subclimax, disclimax, preclimax and postclimax.

Producent—Plants are producents since they produce the food upon which animals live. Animals therefore are consuments.

Psammosere—A sere originating on sand.

Quadrat—A square area of varying size marked off for purposes of detailed study of the vegetation, such as the relative abundance and importance of each species; a number of representative quadrats will reveal the entire range of structure of the entire area.

Reaction—The effect that a plant or community exerts on its habitat.

Regression—Destruction of the existing vegetation by lumbering, fire, grazing, erosion, etc., with subsequent colonization by lower types: not true succession or development from forest to grassland, for instance, but replacement of forest by grassland as a consequence of more or less complete destruction of the trees.

Relict—A species properly belonging to an earlier vegetation type than that in which it is found; a community or fragment of one that has survived some important change, often to become in appearance an integral part of the existing vegetation.

Ruderal—A "weed": an introduced plant species growing under disturbed conditions; native or introduced plants of old fields, waysides, waste places or growing among rubbish.

Saties—A subdivision of a seasonal society (sociation).

Sation—Seasonal groupings of plants and animals within both the sociation and lamiation.

Savanna—The community which characterizes the ecotone between two climax formations; in its most typical expression it consists of grasses and low trees or tall shrubs, or open pine forest and woodland with a grass cover.

Secondary Communities—Communities arising through human interference.

Secondary Succession—Succession on soils denuded of the existing vegetation through the agency of man, such as lumbering, fire, etc.

Seral—Developmental; not static.

Seration—A series of communities produced by a graduated compensation across a valley and operating within a formation or an ecotone.

Serclimax—An early stage in the development of the climax which has been arrested and held stationary for an indefinite period, such as the Everglades of Florida, the cypress-gum swamps of the Gulf Coast, and the tule marshes of California.

Sere—A unit succession, comprising the development of a formation from the pioneer stage through successional stages to the final climax.

Serotinal—Autumnal.

Serule—A miniature succession, such as occurs in fallen logs, decaying stumps, leaf litter, bodies of dead animals, etc. It comprises minute

or microscopic organisms for the most part, and is characteristic of forests in particular, where it serves to return all fallen matter to the soil through the medium of decay and decomposition.

Shinry—Areas of dwarf oak in the southwestern United States.

Sierran—Vegetation of the Sierra Nevada Mountains. (U.S.).

Sociation—A society characteristic of each aspect.

Socies—Societies of developmental communities and of temporary subdominance, such as arrow-heads in a reed-swamp, etc.

Society—A community characterized by one or more subdominants, i.e., species of different life-form from those of the regional dominants; a localized or recurrent grouping of subdominants within a general dominance, such as forbs in grassland that are conspicuous and play an important role in vegetation only at certain times of the year.

Sociule—A seasonal socies of a micro-community.

Specient—An individual of a species.

Stability—The condition in which the plant makes little or no response.

Stabilization—The increase of dominance terminating in a stable climax; it is produced everywhere by progressive invasion typical of succession which culminates in a population most completely fitted for the mesic conditions brought about by the reactions of past plant generations. Such a climax is permanent because of its close harmony with the essentially stable habitat, and will persist just as long as the climate remains unchanged.

Subclimax—The stage in both primary and secondary seres that immediately precedes the climax. An imperfect stage of development, in which the vegetation is held indefinitely either by natural or artificial factors other than climate, such as grazing, burning, cutting, etc.

Subdominant—A species of a lower life-form than that of the dominants of a climax, but which may appear more abundant or conspicuous than the latter at certain seasons of the year. For example, trees and shrubs are more conspicuous in a savanna than the grasses, although the latter are in actual control of the habitat. Similarly, the dominant grasses of the prairie may be more or less concealed during the growing season, by tall forbs.

Subdominule—A subdominant in a micro-community.

Subfluent—An animal member of the biome, of importance comparable to that of a subdominant plant.

Subsere—A sere secondary on areas denuded by man's agency such as lumbering, burning, etc. In regions long settled, subseres form practically the entire cover of vegetation apart from cultivated fields, and even these exhibit the first stage after the annual harvest.

Succession—The process by which the same area becomes successively occupied by different plant communities. Although the movement from initial stage to climax is usually continuous, when one group of dominant plants reaches its maximum, the change is clearly marked.

Taiga—Flat marshy forest; the area between tundra and steppe (Russia).

Transect—A continuous narrow strip that gives a cross section of vegetation. It may be either a line or a belt of a certain width.

Vefluent—An animal member of the biome of minute or microscopic importance.

Xeric—Characterized by, or pertaining to conditions of scanty water-supply.

Xerocline—A dry, warm slope.

Xerosere—A stage in the development of a succession initiated on bare rock, wind-blown sand, rocky talus slopes or other situations where there is an extreme deficiency of water.

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